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HUMAN PHYSIOLOGY

BY

PROF. LUIGI LUCIANI

TRANSLATED FROM THE ITALIAN

WITH A PREFACE BY

PROF. J. N. LANGLEY, F.R.S.

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HUMAN PHYSIOLOGY



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HUMAN PHYSIOLOGY

BY

PROFESSOR LUIGI LUCIANI

DIRECTOR OF THE PHYSIOLOGICAL INSTITUTE OF THE ROYAL UNIVERSITY OF ROME

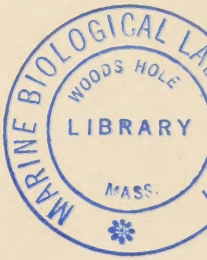
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VOL. IV

EDITED BY

GORDON M. HOLMES, M.D.

THE SENSE ORGANS

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VOLUME V., completing the work, and dealing with Metabolism, Temperature, Reproduction, Stages of Life, Death, and Races of Mankind, is now in the press, and will appear in due course.

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ERRATA

Page 18, table, side-bracket, for "mecodermal" read "mesodermal."
,, 39, line 6, for "stiloid" read "styloid."
,, 63, bottom line, for "ureto-genital" read "uro-genital."
,, 81, lines 15 and 17, for "Aronson" read "Aronsohn."
,, 82, Figs. 27 and 28, for "clitoris of female" read "human clitoris."
,, 84, Fig. 31, for "female clitoris" read "human clitoris."
,, 89, line 23, for "Hansen" read "Hensen."
,, 90, line 12, for "Oley" read "Gley."
,, 130, line 7, for "Panaschi" read "Panasci."
,, 136, line 4, for "Kastel" read "Kastle."
,, 146, line 10 from below, for "$NaBr_2$" read "NaBr."
,, 147, line 15 from below, for "Cu" read "Mn."
,, 162, line 11 from below, for "hairs" read "cilia."
,, 170, line 4 from below, for "Rumsberg" read "Rumberg."
,, 175, line 18 from below, for "sulphate" read "sulphide."
,, 175, line 17 from below, for "phosphate" read "phosphide."
,, 185, line 9 from below, for "hypochloride" read "hypochlorite."
,, 197, line 13 from below, for "Kuss" read "Küss."
,, 203, line 19 from below, for "place" read "plane."
,, 223, line 8, for "Cladni" read "Chladni."
,, 257, line 12 from below, for "Malte" read "Matte."
,, 267, Fig. 106, for "A. E. Schäfer" read "E. A. Schäfer."
,, 269, lines 16 and 23, for "Bruch" read "Brücke."
,, 298, line 12 from below, for "notable" read "not able."
,, 314, line 23, for "paracenthesis" read "paracentesis."
,, 336, Fig. 161, for "G. N. Golding-Bird" read "C. H. Golding-Bird."
,, 351, line 20 from below, for "·0001" read "0·001."
,, 396, bottom line, for "non-parallel" read "a-symmetric."
,, 398, line 7, for "Panigrossi" read "Panegrossi."
,, 410, Fig. 195, for "staircase" read "ladder."
,, 420, line 12 from below, for "Bemessi" read "Benussi."
,, 430, line 19 from below, for "covered" read "coloured."
,, 460, bottom line, for "oniric" read "oneiric."

CHAPTER I

CUTANEOUS SENSIBILITY

CONTENTS.—1. Difference between *modality* and *quality* of sensations. Johannes Müller's law of specific energies. 2. Different intensities of sensations. Weber's law and Fechner's law. 3. Transformation of sensations into perceptions: philosophical theories. 4. Four modalities of cutaneous sensation, according to Blix, Goldscheider, and v. Frey. 5. Cutaneous nerve-endings for sensations of pressure, pain, cold, and heat. 6. Physiological analysis of thermal sensations (heat and cold). 7. Touch and pressure sensations. 8. Capacity for localising cutaneous sensations. 9. Pain sensations. Bibliography.

MOVEMENT and Sensation are the two extremes of the processes of animal life by which the organism is brought into direct relation with the outer world. Movements are always *objective* in character and can be studied directly by external observation. Sensations are invariably *subjective*, and can only be directly analysed by introspection, and indirectly inferred from the expressional movements which are their external concomitants. It follows that the physiology of sensation in man is the necessary starting-point for the comparative physiology of sensation in animals; and the intimate observation of our own consciousness is the only available basis for judging the psychical activities of animals or of other men.

All organs of the body that are supplied with afferent nerves continually send information of their functional state to the central nervous system, and exert a reflex controlling influence along the efferent nerves without passing the threshold of consciousness. At other times they send to the centres messages which are not entirely subconscious, but emerge vaguely and indefinitely in consciousness as a more or less decided sense of well-being or the reverse. Or again, the messages from the different organs to the centres may definitely cross the threshold of consciousness and give rise to distinct sensations which differ in quality and intensity.

The complete excitation or functional activity of a sense is always a psycho-physical phenomenon—that is a physiological

fact intimately associated with special states of consciousness. But very few of the impressions that reach us from the outer world, or from our own body, enter completely into consciousness, because the attention can only be focussed upon a small part of the impressions received.

Sensations are distinguished, according to the most fundamental difference in the psycho-physical phenomena which constitute them, as *internal* and *external*. Internal sensations tell us of the changes within our body and psychical personality; external sensations bring us news of the outer world, or the changes occurring therein.

Internal sensations are always vague, indefinite, and often indefinable in character, even when we are fully aware of them; often, however, they operate unconsciously and modify our mentality, without being distinctly perceived. Such are the sensations of pain, hunger, thirst, nausea, fatigue, sexual desire, etc. The name *coenaesthesia* (from κοινός, common, αἴσθησις, sensation) is often applied to the collective internal sensations aroused in the centres by the excitations that reach them from the viscera, muscles, and surface of the skin.

External sensations are more exact and definite in character, hence they are also known as "specific sensations." They are frequently converted into perceptions, which are objectified sensations, *i.e.* sensations referred to an external cause by a psychical act which includes a judgment, even if an unconscious one. Consequently external sensations are the substrate of all our higher mental functions and all our knowledge.

The physiological neural processes that accompany the sensory phenomena arising out of the activity of the senses are, for the most part, not available to external objective observation; so that in dealing with the senses the physiologist is compelled to borrow freely from the psychological terminology derived from subjective observation, and the missing physiological analysis of phenomena is to some extent replaced by introspective analysis. The justification of this method depends on the validity of the law of psycho-physical parallelism, which assumes not only that functional relations exist between somatic and psychical processes —which is indisputable—but also that for each state of consciousness and each psychical change there is a corresponding state and change in the concomitant neural process—which is not and in the present state of our knowledge cannot be demonstrated. The law of psycho-physical parallelism is thus no axiom, as many have supposed, but is merely an empirical and provisory hypothesis, which enables the physiologist in dealing with the highest functions of the nervous system to remain on the positive ground of controllable laws and phenomena, instead of straying into the region of metaphysics and speculating

on the nature of psychical phenomena apart from any material substrate.

I. The *sense-organs* are the peripheral instruments of our sensations. Most of the sensory nerves are so arranged at the periphery as to present a surface on which the various changes in the environment can operate. With this object the nerve-endings of the sensory fibres are provided with specific mechanisms which are partially non-neural (sense-organs in a strict sense), and are so formed and adapted as only to allow certain definite external alterations to act on and excite the corresponding nerve-fibres, while absolutely or relatively excluding the action of any other form of external stimulation. It is exclusively by means of the sense-organ formed by the eyeball that we perceive those rhythmical vibrations in the ether which we call *light*; it is exclusively by the cochlea of the internal ear that we are aware of the rhythmical vibrations in the pressure of the air that we call *sound*; it is exclusively by the chemical excitation of the olfactory epithelium of the nasal mucosa, or the gustatory epithelium of the lingual mucous membrane, that we are aware of *smell* or *taste*.

The *adequate stimulus* for any given sense is that to which its organ is specially adapted, so that it can receive it and be effectually excited by it; all other kinds of stimuli are *inadequate* for that sense-organ. Light, for instance, is the adequate stimulus for the retina, sound for the cochlea, odoriferous and sapid substances for the organs of smell or taste. Electrical currents, and physical and other mechanical means which can also excite these sense-organs, are inadequate stimuli.

Adequate stimuli are, as a rule, effective only when they act on the peripheral sense-organ; they are not always capable of exciting the sensory nerve directly. The most vivid light fails to excite visual sensation when it falls on the stump of the optic nerve: loud sounds are not perceived by the stump of the auditory nerve, though to this there are some exceptions. Chemical, thermal, and mechanical stimuli can take effect along the course of the olfactory, gustatory, and tactile nerves: but they must be of greater intensity than is required to evoke sensations of smell, taste, temperature, and touch when they are applied to the peripheral end-organ. *Adequate* stimuli therefore become effective only when they act on the terminal sense-organs, which have presumably been adapted to them by a long evolutionary development. *Inadequate* stimuli, on the contrary (so far at least as we know), can act on any part of the sensory nerve along its course, and are less effective, or even ineffective, when applied to the peripheral sense-organ.

Little is known at present about the specific arrangement of the sense-organs, whereby they are specially excitable or sus-

ceptible to one particular stimulus while absolutely or relatively inexcitable to stimuli of other kinds. It is not a sufficient explanation of this fact to say that in certain cases the influence of the inadequate stimuli is hindered or impeded by the topographical position of the sense-organs. The auditory apparatus, for example, is shielded from the action of light, of mechanical impacts, of various vapours; the visual apparatus is well protected from mechanical and chemical stimuli. On the other hand, the auditory cells are perfectly accessible to sound-waves, the visual cells to light, the olfactory cells to the air inspired, the gustatory cells to the food-stuffs ingested. These statements, which neglect the internal constitution of the sense-organs, fail to explain the specific susceptibility of the latter to given stimuli. What is the intrinsic organic condition that prevents the peripheral organs of taste and smell from reacting to light, warmth, or mechanical pressure (which are adequate stimuli for the visual and cutaneous nerves), while they are excessively sensitive to certain chemical stimuli? From the teleological point of view, we know this must be so. If it were otherwise, if the organs of taste and smell were not specifically predisposed to react to chemical stimuli, but reacted with the same facility as the skin to heat, contact, and pressure, they would be incapable of conveying to our consciousness any precise intimation of the nature of the chemical stimuli to which they are adapted. The same may be said of the specific adaptation of the retina to light, the cochlea to sound, etc. But even if the teleological connection between the specific nature of the sense-organs and their specific function is plain, we are still ignorant as to the internal nature of their respective structures, on which depends their specific excitability to different kinds of stimuli. In all probability, as Fick assures us, there are in the peripheral sense-organs compounds of a highly unstable molecular constitution, which are decomposed by slight impacts, and thus develop energy which acts on the nerve as an effective stimulus.

The senses can be distinguished and classified either by their anatomical situation, or by the nature or quality of the stimulus adequate to excite them, or lastly, by the kind of sensation which they arouse in consciousness. These different categories mostly coincide. Thus vision is the sense of the eye, for which the adequate stimulus is light, which produces visual sensations; hearing is the sense of the ear, and is excited by tones and noises which arouse auditory sensations in consciousness; taste is the sense of the tongue, and is excited by sapid substances that arouse gustatory sensations; smell is the sense of the nose, and is excited by odorous substances which evoke olfactory sensations. But when we apply the anatomical test we must further distinguish a cutaneous sense, a muscular sense (inclusive of tendons and joints), and a visceral sense; according to the nature of the stimulus, we

must add to the cutaneous sense a pressure sense, a temperature sense, and a pain sense; lastly, according to the quality of sensation, the thermal sense must be subdivided into a heat sense and a cold sense. The psychological classification, founded on the dissimilar nature of the sensations, is evidently the most analytical and, therefore, the most rational to employ in defining and distinguishing the sense-organs.

It is important to notice that two kinds of dissimilarity can be distinguished in the comparative study of sensations. Helmholtz (1879) made a distinction between differences in modality and simple differences of quality. Sensations of different modality are so fundamentally dissimilar that transition from one to the other is not possible; no degree of similarity, nor even a simple relation of intensity, can be established between them. No one, for instance, can say whether a given musical tone resembles more closely the colour red, or a bitter taste, or the scent of musk; nor decide whether the light of a candle is stronger or weaker than the sensation evoked by a certain solution of sugar, a given musical note, a sensation of pressure or temperature in the skin. If, on the other hand, we compare the sensations appreciable within each modality, we can indeed recognise qualitative differences; but these are not so profound as to make impossible a reciprocal transition from one to the other, or a comparison and judgment of their greater or less similarity, greater or less intensity. Two separate auditory sensations may be qualitatively distinguished by their difference of pitch; it is also possible to judge which of them is the stronger. The colours of the spectrum not only present a gradual transition from one to the other, but we can also appreciate their greater or less resemblance or their relative brightness.

The differences between the modalities of sensation observed on examining the higher sense-organs of vision and hearing, both in their mutual relations and in the relations between each of them and the lower sense-organs, could not well be more profound and striking. But this conspicuous disparity does not appear on comparing the sensations that arise from the less well-developed sense-organs.

Fick (1879) first pointed out that the sensations of smell, taste, touch, temperature, and pain are modalities not so different in themselves that a gradual transition from one to the other is impossible. Thus, between the sensation of pricking produced by pepper on the tongue and that produced by a solution of table salt, the former being a tactile and the latter a gustatory sensation, a gradual transition is possible by means of a series of salt solutions and pepper extracts of increasing strength. In this case, therefore, the difference in modality assumes the character of differences in quality, between which a gradual transition is possible, as between the colours of the solar spectrum.

This in no way invalidates the distinction between modality and quality of sensation; it merely emphasises the fact that in the higher senses the differentiation in the modality of the sensations is far more pronounced and striking than in the less developed senses.

The different modalities of the sensations do not depend on differences in the external stimuli which excite them, but on the specific nature of the different senses. Johannes Müller (1840) published a masterly development of this theory, and brought out its full importance alike in physiology and psychology. It is usually known as the "*Law of specific energy of the senses*" (vol. iii. p. 262), and was summed up by Müller in the following general propositions:—

(*a*) "No kind of sensation can be produced by external causes which cannot be equally excited in the absence of external causes by intrinsic changes in our nerves."

Purely internal causes may give rise to sensations of cold, heat, pain, pleasure, which are normally evoked by external stimuli acting on the skin. Certain olfactory and gustatory sensations are termed subjective, because they arise in the absence of any substance capable of arousing smell or taste. Auditory sensations may be due to internal or external causes: buzzing and subjective noises in the ear are common at the beginning of feverish disorders. Visual sensations—light, darkness, and colours—may occur without extrinsic causes. When the excitability of the optic nerve is exaggerated, subjective sensations of light and colour arise even with the eyes shut and in total darkness. Independently of transmission of any stimulus from the peripheral organs the nerve-centres may be thrown into activity by direct internal excitation. Under physiological conditions this happens in *dreams*, under pathological conditions in *hallucinations*. The outer world can therefore make no impression on us which purely internal causes are unable to arouse.

(*b*) "The same internal or external cause evokes different sensations through the different senses, according to their nature or their specific sensibility."

Hyperaemia or congestion of the sense-organs is an internal cause which produces specific effects on the different senses, as buzzing in the ear, flashes of light in the eye, pain in the sensory nerves of the skin or viscera, etc. The electrical current is a classical means of showing that the same external cause may produce sensations of dissimilar modality when it acts on different senses. If applied to the eye the galvanic current evokes luminous sensations, to the nose smell, to the tongue taste, to the skin sensations of pressure, warmth, cold, or pain, according to the nerve-organs encountered at the different parts to which it is directed.

(*c*) "The specific sensations of each sensory nerve can be evoked by different internal and external stimuli." . . . "Sensation is not the transmission to consciousness of a quality or state of an external body but of the quality, or the state of a sensory nerve as produced by an extrinsic cause, and these qualities differ in the different sensory nerves."

Many attempts have been made, both by the predecessors and by the successors of Johannes Müller, to explain the capacity of the different sensory nerves for receiving certain impressions, by ascribing to them a specific excitability to certain stimuli. This hypothesis is inadequate to explain the facts. We have seen that each sensory organ has an "adequate stimulus," that is, is specifically predisposed to become excited by a given stimulus. But this does not prevent its being excited also by other stimuli which we have termed "inadequate." Mechanical or electrical stimulation of the chorda tympani of man at the point at which it passes through the tympanic cavity excites sensations of taste at the tip of the tongue. The electrical current is not an adequate stimulus of any sense-organ; there is no special sense-organ for this physical agent, as, *e.g.*, the eye reacts to light, or the ear to sound. Yet electricity is capable of exciting every sense-organ, and evokes different sensations in each. We are therefore compelled "with Aristotle to attribute to each sensory nerve distinct energies, which are its vital qualities, just as contractility is the vital property of muscle. The sensation of sound is thus due to the specific energy of the auditory nerve, light and colour to that of the optic nerve, etc." (Müller). When a certain number of air-vibrations impinge upon the auditory organ, they produce a sensation of sound; when ether vibrations of a certain wave-length fall on the visual organ, a sensation of light results; but sound and light as sensations are not comparable with the vibrations of the air or ether. The same vibrations of a tuning-fork that produce a note in the ear excite a sensation of vibration in the skin; the same ether waves streaming from a lamp produce light through the eye and a sensation of warmth on the skin. In order to obtain sensations of sound or light not only the vibratory movement of the air or ether, but also the presence of an auditory or visual organ, is indispensable. "Without the living ear there would be no sound in the world, but only vibrations. Without the living eye there would be no brightness, no colour, no night, only the oscillations of the imponderable matter of light, or the absence of them" (Müller).

How does the excitation of the sensory nerves arouse the different conscious sensations in the brain? Of what character is the active state of the sense-organs which generates in us the different modalities of sensation? In every age philosophers

have sought to answer this question, but no reply is possible from the standpoint of experimental science. This is one of the transcendental problems to which Du Bois-Reymond replies *ignoramus et ignorabimus*. But the same answer had already been given by his master Johannes Müller. "The nature of this state of the nerves whereby they see light, hear sound, the nature of sound as a property of the auditory nerve, of light as a property of the optic nerve, of taste, smell and touch, remain eternally unknown like the final causes in natural philosophy." The modern philosophical principle of the relativity of all knowledge acquired through the senses is a direct consequence of Müller's law, that our sensations depend upon the innate qualities of our senses, and do not reproduce the phenomena of the outer world.

(*d*) "We do not know whether the different energies of the sensory nerves are intrinsic in them or in the parts of the brain and cord to which they run, but it is certain that the central portions of the corresponding sensory paths within the brain are capable of exciting the corresponding sensations, independently of the nerve-conductors." This conclusion leaves the question undecided whether the specific energies of the senses depend upon a property inherent in the respective sensory nerves or upon their central terminal organ. As we have already seen (iii. p. 262), this question is still unsolved, though the theory Johannes Müller himself preferred receives most support, viz. the *identity of nervous function*, on which the nerves are regarded merely as indifferent conductors to the centres of the excitations that arise in the peripheral organs. The specific excitability of the several senses to given stimuli is due to the differentiation of the protoplasm, which is in relation with the nerve-endings of the peripheral sense-organ; the specifically distinct sensations that arise in consciousness during excitation are due to the dissimilar nature of the central organs; the sensory nerves that unite the peripheral organs with the central sense-organs are uniform conductors which are identical both in their internal structure and in their function. Hering, nevertheless, maintains the contrary hypothesis, and extends the concept of specific energy not only to the central cells but also to their processes, *i.e.* to the whole neurone.

It is very difficult to determine the limits of the law of the specific energy of sensory nerves. The question is whether not modality only, but also the qualitative differences that occur within one and the same modality of sensation, depend on specific energies of the neurones that build up the sensory organ, or whether they can be explained on the assumption that the individual fibres of a sensory nerve are capable of serving different forms of excitation or activity. This question will be discussed in relation to each of the several senses.

II. It is only within certain limits of intensity that external agents are effective stimuli. The minimal strength which is necessary to produce a sensation is known as the *liminal intensity*, or *threshold stimulus*. The least perceptible increase of stimulation beyond this value is termed the *liminal difference*, or *threshold of difference*. Every increment of stimulus up to a certain maximal limit produces an increase of sensation. The maximal sensation is obtained with a comparatively low strength of stimulus. Every increment of stimulus above that point not only fails to increase the sensation, but actually induces fatigue or exhaustion of the peripheral sense-organ, which is the more rapid and complete in proportion as the stimulus is excessive.

The judgment we are able to form as to the intensity of a given sensation and the quantitative relation between the stimulus and the sensation is necessarily only approximate. We cannot state how much stronger or weaker one sensation is than another; we can only say whether a sensation is stronger or weaker than, or equal to, another.

Speaking generally, it may be said that sensation increases—within certain limits—with the strength of stimulus, but not proportionately to it; doubling or trebling the stimulus does not double or treble the intensity of the sensation. Common observation shows, in fact, that one and the same stimulus is perceived more, or less, or not at all, according to the conditions under which it takes effect. In the silence of night we perceive the ticking of a watch, while in the noise of day we scarcely hear the voice of any one speaking to us, and the clatter of the railway may prevent us from hearing our own voice. This means that the least stimulus can be perceived when the pre-existent sensation is feeble, and that a much stronger stimulus is required when the organ is excited by a previous strong stimulation. It is therefore obvious that intensity of sensation does not increase proportionately to strength of stimulus, but much more slowly. In order to determine the exact quantitative relation between stimulus and sensation it would be necessary to measure the intensity of both by the same methods. And as any such direct measurement of sensation is impossible, the only attempt we can make at solving the problem is to determine the threshold of difference, *i.e.* how much the strength of stimulus must be increased in order to obtain a perceptible increase in the intensity of the sensation.

E. H. Weber (1831) first attempted this estimation. While testing the power of discrimination in musculo-cutaneous sensibility he met with a surprisingly simple result: the increase of stimulus necessary to produce an appreciable increase in sensation bears a constant ratio to the total stimulus, *i.e.* is always the same fraction of the total intensity of the stimulus. Thus to appreciate the minimal increase of a weight held in the hand, it is always

necessary to add the same fraction of the weight (average $\frac{1}{17}$, according to Weber), whatever its absolute value—whether in ounces, pounds, grammes, or kilogrammes.

Later observations by a number of investigators have proved that, within certain limits, Weber's law is approximately valid for all the different modalities of sensation, provided stimuli of medium strength are employed. On the other hand, there are more or less marked exceptions to the law when the stimulus is too strong or too weak. Generally speaking, Weber's law expresses a fact of great empirical importance, but has no claim to be a method of *absolute measurement* of sensation, or of exact determination of the ratio between sensation and stimulus.

The same cannot be said for the so-called "*psycho-physical law*" which Fechner (1860) formulated as a larger generalisation from Weber's law. According to Fechner, if the increase of the sensation is proportional to the increase of the stimulus divided by the absolute intensity of the excitation, the sensations will stand in the same ratio to the stimuli as do logarithms to their numbers. Let S be the sensation, R the stimulus, C the constant represented by the liminal difference, and Fechner's "formula of psycho-physical measurement" is obtained: $S = C \log R$, *i.e.* sensation is proportional to the logarithm of the stimulus.

Fechner's theoretical interpretation of Weber's law is open to serious objections. Fechner assumes that the value of the liminal difference remains the same at all points of the scale (S_Δ = constant), while experiment shows that Weber's law only holds good within certain limits, and that the value of S_Δ alters at the extremes of the strength of stimulus. Fechner further assumes that the smallest appreciable increase of a sensation represents its *unit of magnitude*, and that all sensations result from different sums of such units, which is a purely arbitrary interpretation of Weber's law, supported neither from introspective investigation nor from physiological observation. It is one thing to state with Weber that the relation between the appreciable increase of a stimulus and its absolute magnitude is constant—within certain limits—and quite another to say with Fechner that every appreciable increment of stimulus invariably excites a sensation of the same value, and that these sensations together summate into a complex whole. The idea of giving a numerical measure of sensations is, according to William James, purely and simply a mathematical speculation upon eventual possibilities, which has never found any practical application. The psycho-physical law will always remain a fossil in the history of psychology.

III. Up to this point we have discussed *sensations*, and their different modalities, qualities, and intensities. But psychologists

mean by the term "sensation" the simplest and indivisible state of consciousness, by which we appreciate any alteration, *e.g.* light, colour, a sound, a taste, etc., without associating with it any relation to internal or external causes. Pure and simple sensations, as such, exist only in the new-born, in whom the sensory centres are incompletely developed. In adults, *sensations* are converted by a psychical process into *perceptions*, which are a complex of co-ordinated elementary sensations, by which we not only perceive the changes in our state of consciousness but are able to interpret and to objectify them. A simple tactile sensation, for instance, is inevitably connected with an external body coming into contact with the skin; a sensation of bitterness with the presence of something in the mouth; a sensation of sound or colour with the presence of a sounding or a coloured body in the outer world, and more or less remote from us. Each of our sensory perceptions, though composed of a complex of elementary sensations which are more or less distinct from each other, nevertheless presents itself as a kind of unit in our consciousness. In the physiology of the senses it is often no easy task to distinguish in apparently simple sense-perceptions the elementary sensations of which they are composed.

The objectifying of perceptions, by which we refer the changes in our senses to external causes acting on them, is a fundamental characteristic common to all perception. The tendency to project our perceptions externally varies in the different senses. It is strongest in the higher senses of vision and hearing. Common visual and auditory perceptions appear unmistakably as properties attaching to external objects, more or less remote from us, apart from any appreciable sensation of change in our visual or auditory organs. The perceptions of the lower senses, touch, temperature, taste, and smell, have less tendency to projection. Tactile perceptions are, as a rule, projected to the place where the object that excites the cutaneous sense-organ is situated, and we are clearly able to distinguish the sensation of the external object that comes into contact with the skin from the change in the sensory surface. In the sensation produced by a warm body we may be uncertain whether we feel the heat of our skin or of the external object. So too in sensations of taste or smell, it is doubtful whether we are most aware of the changes in the tongue and nasal mucous membrane, or of the presence of the sapid or odorous substance.

More important, however, than the greater or less degree to which normal sensory perceptions are projected beyond us, or to the peripheral sense-organs, is the fact that both subjective and hallucinatory perceptions, and also the effects of experimental or pathological stimulation of the sensory nerve-trunks, are projected externally: we refer them not to the place at which they are really excited, but to that to which we are accustomed to

refer the corresponding normal peripheral excitations, as was shown in the chapter on the general physiology of the nervous system (Vol. III. p. 201).

This leads us to grave philosophical questions which can only be briefly touched on. How does the objectification of sensory perceptions come about? How are we able to distinguish the outer world from ourselves? Since we do not actually feel external objects, but only the changes which these effect by means of the sensory nerves and sense-organs in the sensory centres—which changes are quite different from the external objects—why are we convinced that our senses are not deceiving us? These problems are as important as they are hard to solve, and the interpretations given to them by psychologists and physiologists differ widely.

In all ages the theory that the whole of our sensations and our fundamental notions of the external world are but illusions and phantasms of the mind has had many followers. Its most extreme form is the *absolute phenomenalism* of Hume. This obviously does not solve the question as to the origin of perceptions and ideas, nor does it explain the common belief in the reality of the external world.

Kant's *critical idealism* was a reaction from this theory. The phenomena of the outer world have nothing in common with our sensations. We can know nothing about the true nature of the external world: the only things we can know directly are the states and phenomena of our consciousness. We can only conceive of the external world by the aid of physical hypotheses and speculations—such as the undulatory theory, the atomistic hypothesis, the mechanical theory of heat, etc. Perceptions and ideas depend essentially upon congenital predispositions of the senses and the brain, and on original or innate properties of the mind.

In opposition to this critical nativistic idealism is the sensory empiricism which assumes that ideas are the result of observation and education of the senses. Locke, Condillac, John Stuart Mill deny the existence of *a priori* ideas. Everything comes from experience or activity of the senses: the soul deprived of any experience is a *tabula rasa*. Sensations are merely simple signs representative of external objects, different indeed from them, but always interpreted in the same way, from which we always deduce the existence and properties of external objects by the aid of previous observations.

Helmholtz, who partially accepted this theory, recognised its inadequacy to explain the facts, and assumed with Schopenhauer that all our perceptions and ideas presuppose the a-priority of the causal concept without which we cannot look upon objects as the extrinsic cause of our sensations. This theory was further

developed by Herbart and Wundt, the first of whom specially brought out the importance of *association* of the various sensations and perceptions, while the second laid stress on the *unconscious reasoning processes.*

The new-born infant only possesses internal sensations, such as hunger, satiety, etc. Its visual, auditory, tactile and other sensations are only perceived as changes of its own being, and are not referred to the causes by which they are produced, nor projected externally. By degrees, however, it begins to notice various objects and accommodate its eyes for distant vision. Simultaneously the child moves its limbs and begins to exercise its cutaneous and muscular senses. Tactile sensations are at first perceived as internal sensations, as obstacles to movement; but the eye perceives the movement of the hand, and the coincidence of visual and tactile sensations soon leads, by an unconscious process of reasoning, to the conviction that the object perceived by both senses is one and the same. Apart from the association of the two senses, touch alone is sufficient by unconscious judgment to teach the babe to distinguish its own body from the outside world. When the hand comes in contact with another sensitive point of the skin, it receives a double sensation; when, on the contrary, it touches an extraneous object, it is aware of one sensation only.

For the adequate discussion of these and other problems the student must turn to text-books of psychology. Here we must confine ourselves to saying that the transformation of sensations into perceptions is still a wholly mysterious process, even if it can reasonably be said to depend on and be favoured by the combined activity of all the senses.

IV. The whole surface of the skin and the visible parts of the mucous membrane have important sensory functions which have long been grouped together under the common denomination of "tactile sensation," without regard to analysis of the different qualities of sensation. For this reason, perhaps, the study of these functions remained stationary for a long time, down to the last decades of the nineteenth century, when a conspicuous advance was made.

Pechlin (1691) was the first who insisted on the anatomo-physiological distinction between tactile and thermal sensibility (*caloris et frigoris sensus*). Erasmus Darwin (1794), in his famous *Zoönomia*, proposed the same distinction, and adduced as evidence the case of a patient suffering from abolition of tactile sensibility, in whom the appreciation of warmth was normal. But this attempt to distinguish between the different cutaneous sensations was neglected until E. H. Weber (1834) undertook the systematic study of the physiology of cutaneous sensibility, and, after prolonged original and methodical research, obtained

valuable results which still constitute an important part of our knowledge of this subject.

A new era in the physiology of the cutaneous senses was reached by the discovery of *heat, cold*, and *pressure spots* by Blix (1882), confirmed by Goldscheider (1883) and Donaldson (1885). Another marked development of the physiology of the cutaneous senses was the work of v. Frey (1894–97), which showed that in addition to the above there also existed in the skin a fourth sense-organ constituted by *pain spots*.

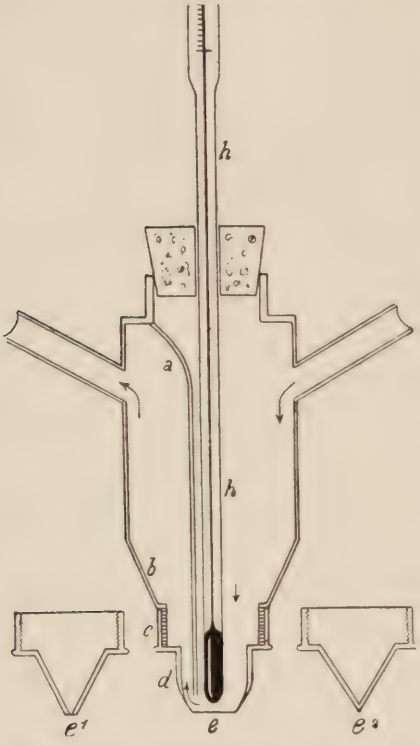


FIG. 1.—Thermo-aesthesiometer of Veress, seen in section. The instrument consists of a hollow metal cylinder 4 cm. in diameter, divided internally by a metal plate (*a*) into two unequal parts, into one of which is inserted the tube for inflow, into the other that for outflow of the hot or cold water. At *b* the cylinder becomes conical. At *c* the terminal part *d* is screwed on, to carry the exciting surface *e*, which is applied without pressure on the skin. The end of a thermometer *hh*, to measure the temperature of the circulating water, is passed through the cork which closes the top of the apparatus. The exciting surface may be varied by using the alternative pieces e^1, e^2.

The work of Herzen (1886) and Goldscheider (1898) on the paralysis produced by compression of the nerves of a limb also lent support to the theory that there are specifically distinct nerves and organs of sensation in the skin; sensibility to cold and to pressure are more strongly depressed and disappear more rapidly than sensibility to heat and pain. Ponzo (1909) showed that stovaine by its peripheral action produces local anaesthesia to stimuli of touch, pain, and cold, while sensibility to heat stimuli is retained. In this respect the work of Stranskys (1899) on the reappearance of sensibility in portions of skin grafted for surgical purposes is of great importance. It proves that tactile or pressure sensibility appears first, while sensibility to pain and to temperature develop later in the transplanted portions of skin.

It is still uncertain whether in addition to the four modalities of cutaneous sensation, viz. the sensations of contact or pressure, of cold, of warmth, and of pain, other independent qualities of sensation should be admitted, such as itching, tickling, sexual

pleasure, etc., or whether these should be considered as special modifications of the senses of touch and pain.

A clear idea of the form, arrangement, and number of the different sensory points on the skin may be obtained by briefly reviewing the experiments on which the discoveries of Blix, Goldscheider, and v. Frey were founded.

The simplest apparatus will serve for investigating heat and cold spots. Small metal rods with blunt ends, that can be dipped into cold or hot water, would be suitable, except that they have to be changed so frequently, and that it is impossible to be certain that they always act on the skin at uniform temperature. The contrivance of Blix, which consists in a small hollow metal cylinder, through which flows a constant stream of water at uniform temperature, is more reliable. Alrutz and Kiesow made various alterations in this apparatus, so that it can be used for different purposes. The most perfect is the thermo-aesthesiometer of Veress (Fig. 1), which is used for mapping out the thermal sensibility of small cutaneous areas of 2 or 6 mm. The end of the apparatus can be unscrewed and readily replaced by surfaces of different sizes, or by a blunt point, when required for the investigation of heat spots.

For pressure points the simplest and easiest method is that of v. Frey—with the so-called exploring hairs or bristles. Hairs of varying thickness (horse-hair, woman's hair) are fixed to the end of a rod, the length of which varies from 1 to 4 cm. Fig. 2 gives the latest form of v. Frey's hair-aesthesiometer. The anterior graduated half of the metal cannula runs backwards and forwards, so that more or less of the hair is covered. If the point of the hair is placed on, and vertically pressed against, the scale-pan of the balance, the amount of pressure necessary to bend it lightly can be determined; this, of course, increases or diminishes according as the length of the hair is less or greater. The millimetre scale of the instrument serves for the empirical graduation of the degree of pressure required to bend the hair according to the length of the exposed portion.

The same aesthesiometer may be used to determine pain points if the exposed portion of the hair is so short that it will bend only at a pressure sufficient to evoke a sensation of pricking.



Fig. 2. -Hair-aesthesiometer of v. Frey. Explanation in text.

If a moderately cool metal point is brought into contact with the skin, without pressure, the sensation of cold is evoked only at circumscribed spots, distant 1-2 mm. from each other. These are the *cold spots* of Blix. If the metal point used for exploring the skin is much cooled, a sensation of cold can also be obtained from other surrounding areas of the skin; but it is always less intense, proving that it depends on transmission of the stimulus to the true cold spots. If the skin is tested with a hot metal point, sensitive spots are found which react in the same way by sensations of warmth. These are the *heat spots* of Blix. Exploration of the skin with gentle tactile stimuli, as by hairs, gives Blix' *pressure spots*. Finally, the same method will detect v. Frey's *pain spots*.

These numerous sensitive points for cold, heat, pressure, and pain are not superposed, but are distributed over different parts of the skin. Fig. 3 shows that Blix' points for cold, heat, and pressure are not really spots, but that the sensation spreads round them as though due to a sort of irradiation of the stimulus, so that the sensory points resemble small placques. These sensory points are not equidistant nor regularly distributed, and consequently

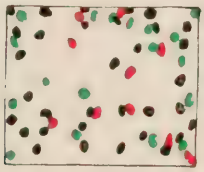


Fig. 3. — Distribution of specific sensory spots on skin of the dorsal surface of the left thumb. (Blix.) Cold spots coloured green, warm spots red, pressure spots black.



Fig. 4.—Distribution of thermal spots on palmar surface of left forearm. (Kiesow.) Cold spots marked green, warm spots red.

there are insensitive areas of skin of varying extension between them. The cold points are much more numerous than the heat points, and the pain points (not shown in Fig. 3) more numerous again than the points for contact or pressure.

The number of points is much greater according to Goldscheider than to Blix. Kiesow's accurate researches show that the data of the latter are more reliable: he proved that the cold spots of Blix may be analysed into groups of individual cold points. Fig. 4

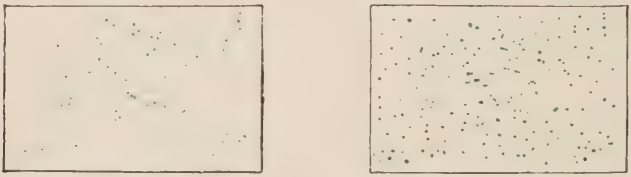


Fig. 5.—Distribution of cold and tactile spots on dorsal surface of left wrist. (Kiesow.) Cold spots marked green, tactile spots black. The left-hand figure only contains cold spots, the right-hand cold spots and tactile spots in the same area.

gives the distribution of the thermal points according to Kiesow on the palmar side of the left forearm, Fig. 5 the distribution of cold points and tactile points on the dorsal side of the left wrist.

Kiesow further found that in regions provided with hairs the cold spots invariably lie near the tactile hair spots but do not coincide with them. He concludes that the vicinity of cold spots to the hair is in relation with the so-called "goose-skin" produced by the contraction of the pilo-motor muscles; it is presumably due to a reflex arc.

Sommer continued these studies and found in 1 sq. cm. of adult skin 6-23 cold spots and 0-3 heat spots; on an

average, therefore, 12-13 cold spots and 1-2 heat spots per sq. cm.

Blix found that in the hair-clad regions of the skin, which he estimates at about 95 per cent of the whole, the pressure points coincide with the hair papillae; other pressure points that can be detected here and there where there are no hairs probably correspond to rudimentary hair papillae. But the tactile surfaces proper, where the touch spots are closely arranged, are found in the regions that have no hairs — particularly the tips of the fingers, palm of the hand and sole of the foot, red part of the lips, tip of the tongue, etc. The number of pressure points, according to v. Frey, averages 25 to each sq. cm., except on the head.

The number of pain points has not yet been estimated. On the back of the hand v. Frey found 100-200 in every sq. cm.

Once the position of the sensory spots on any part of the skin is fixed by means of fast colours, it is easy not only to identify them at any time, but also to verify on them Müller's law of the specific energies—by showing that they react by the same form of sensation (warmth, cold, pressure or pain) when excited not only by adequate but also by inadequate stimuli. Sensations of cold, *e.g.*, are obtained by exciting the corresponding spots not only with a cold point but also with a mechanical or electrical stimulus, or with a point heated to 45°—v. Frey's *paradoxical sensation of cold.*

The legitimate conclusion from these results is that the skin is provided with at least four distinct sets of sensory nerves, for the sensations of cold, warmth, contact or pressure, and pain; that these nerves terminate within the skin in special peripheral sense-organs; and, lastly, that the sensitive points of the cutaneous surface correspond to these sense-organs in the layers below them.

V. Before attempting to solve the question whether four different organs or terminal corpuscles correspond with the four forms of cutaneous sensation, we must refer to the latest morphological work on the nerve-endings in the skin.

The sensory nerve-fibres that innervate the skin form a deep nerve-plexus in the subcutaneous panniculus adiposus. Most of the fibres of this plexus run towards the surface of the skin, and after crossing the reticular layer of the cutis reach the subpapillary layer, where they form a second plexus less rich in fibres, the so-called superficial cutaneous nerve-plexus. A deep vascular network corresponds to the deep nerve-plexus; a superficial vascular network to the surface plexus.

Fibres are given off by the deep plexus which terminate after a short course in special corpuscles or peripheral sense-organs situated in the panniculus adiposus. From the superficial nerve-plexus still more numerous fibres branch off to end in special corpuscles in the different layers of the cutis — the reticular,

subpapillary and papillary layers. Some nerve-endings even reach the rete mucosum of the epidermis, more exactly the stratum germinativum or layer of cylindrical cells and the prickle or polyhedral cells, where they end not in complex corpuscles but in simple swellings or bulbs.

The following table from Ruffini, adopted also by Crevatin and Dogiel, indicates the topography of the different nerve-endings present in the various layers of human skin:—

Epidermis (ectodermal origin)	Stratum corneum		Layers without nerves.
	Stratum lucidum		
	Rete mucosum	Stratum granulosum	
		Layer of prickle cells	Layers of longer nerves.
		Stratum germinativum	Hederiform expansions.

Cutis vera (mucodermal origin)	Basement or supporting membrane.	
	Papillary layer	Meissner's corpuscles. Dogiel's corpuscles. Ruffini's papillary endings. Golgi-Mazzoni corpuscles.
	Subpapillary layer	Meissner's corpuscles. Dogiel's arboriform terminations. Golgi-Mazzoni corpuscles.
	Reticular layer	Dogiel's arboriform terminations.
	Layer of panniculus adiposus	Pacini's corpuscles. Golgi-Mazzoni corpuscles. Ruffini's organs. Dogiel's arboriform terminations.

As shown in this table, the most superficial nerve-endings of the skin lie in the two deepest layers of the rete mucosum or Malpighian layer. Langerhans (1868) first saw that certain nerve-fibres, after losing their myelin sheath, penetrate the epidermis to form a network with loose meshes, and then spread in independent and varicose branches through the epithelium, to the outer limit of the layer of prickle cells, where they terminate in bulbs (Fig. 6). Phylogenetically, these represent the oldest form of nerve-endings in the vertebrate epidermis.

The so-called hederiform nerve-endings lie in the Malpighian layer close to the sweat-glands. The nerve-fibres of which they are formed come from the superficial plexus of the skin. Near the epithelium they lose the myelin sheath, and divide into branches, which spread and twist between the prickle cells and terminate—according to the latest work of Dogiel—in baskets or nets (Fig. 7). Frequently, but not always, a cell of peculiar appearance is found within the basket, which Ranvier and Dogiel

believe to be sensory in character, like those found in the olfactory

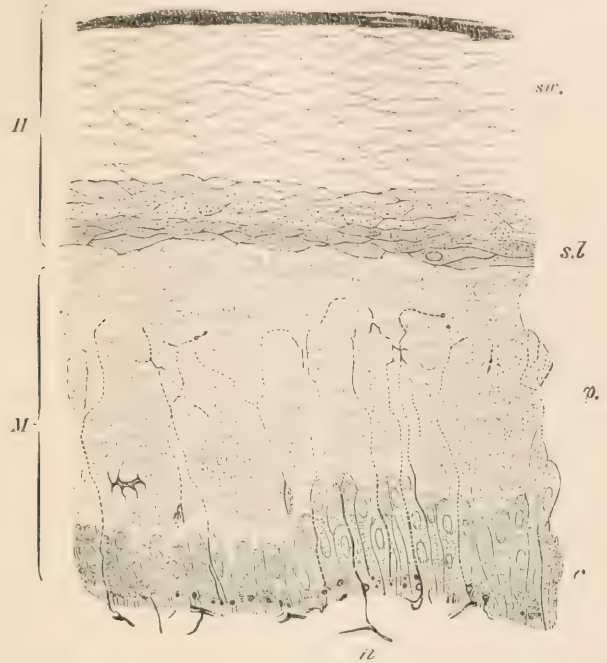


FIG. 6.—Section through epidermis of human hand. (Ranvier.) *H.*, Horny layer: consisting of *s.*, superficial horny scales; *sw.*, swollen horny cells; *s.l.*, stratum lucidum. *M.*, rete mucosum or Malpighian layer: consisting of *p.*, prickle cells, and *c.*, elongated cells forming a single stratum near the corium; *n.*, part of a plexus of nerve-fibres in the superficial layer of the cutis vera; from this plexus varicose nerve-fibrils can be traced between the cells of the Malpighian layer.

and gustatory organs. Phylogenetically, the hederiform endings



FIG. 7. Dogiel's small intra-epithelial baskets, seen in profile. These consist of ramifications of varicose myelinated nerve-fibrils, which become expanded in contact with the prickle cells.

with terminal baskets represent the latest form of nerve-ending in the vertebrate epidermis; they occur only in mammals.

Meissner's corpuscles, which lie in the papillae and subpapillary layer of the corium, were discovered in 1852 by Meissner and R. Wagner in the cutaneous papillae of the hands and feet. Their structure is complex and very variable, so that, according to Ruffini, each corpuscle requires special description. They are found in man and the ape, but have not been recorded in other mammals. Usually they are oval or rather elongated. One, two, or more medullated fibres run to the corpuscle and penetrate its interior after winding round it once or twice, lose the myelin sheath and the sheath of Schwann, and then form a spiral coil with a number of more or less irregular convolutions. The branches of the axis-cylinder which make the spiral are often very varicose, and have one or two terminal enlargements (Fig. 8). The non-nervous tissues of the corpuscle consist in an external capsule of lamellated connective tissue, and a homogeneous, finely granulated interior, which is probably formed of fibrillary connective tissue, with a number of nuclei.



FIG. 8.—Meissner's corpuscle in a papilla from the skin of the hand, stained with gold chloride. Highly magnified. (Ranvier.) *n*, *n*, two nerve-fibres, passing to the corpuscle; *a*, *a*, terminal varicose ramifications of axis-cylinder within the corpuscle.

Many varieties of Meissner's corpuscles are known. Those last described by Dogiel represent a transitional form between the typical nerve-endings of Meissner, which are collected in a corpuscle enclosed in a capsule, and the non-typical nerve-endings, which do not form real corpuscles, but remain free within the papilla, without a surrounding capsule: these were first described by Ruffini (1892) in the papillae that contain no Meissner's corpuscles, under the name of papillary bulbs. Dogiel's corpuscles consist of two parts: one closed, lying at the base of the papilla, the other open towards its apex. The former differs in no respect from the typical Meissner's corpuscle, the latter resembles one of the many forms of free nerve-endings described by Ruffini, Sfameni, and others (Fig. 9).

Special corpuscles were described by Golgi (1880) in peritendinous connective tissue and the external perimysium of human muscle. These were thoroughly investigated by Mazzoni (1891), and are therefore known as the Golgi-Mazzoni corpuscles. Ruffini (1894) discovered that they are also present in subcutaneous connective tissue, as well as in the subpapillary and papillary layers. Their external form and dimensions vary; they consist of a lamellated capsule and an internal core of fibrillary connective tissue

with many nuclei. Two or more branches of a nerve-fibre penetrate the core, and there lose their sheath and become attenuated. The pale fibres divide and subdivide into a large number of branches, which do not form twisted convolutions, but run a tortuous course to the end of the core. The branched fibres for the most part present numerous varicosities of different shapes



FIG. 9.—Dogiel's corpuscle. *a*, Varicose fibre, passing to the corpuscle; *b*, *b*, closed portion of corpuscle, corresponding to the base of the papilla; *c*, free part, corresponding to the apex of the papilla, formed of non-myelinated varicose fibres.

and sizes (Fig. 10). In others the varicosities are scanty, and the appearance of the terminations is totally different (Fig. 11). In others again, according to Crevatin and Dogiel, one or more delicate non-medullated fibres also enter the corpuscle, where they ramify and form a slender plexus at the periphery of the core, and also penetrate inside and mingle with the ramifications of the myelinated fibres (Fig. 12).

In the subcutaneous fatty tissue there are two other characteristic forms of corpuscles besides the Golgi-Mazzoni bodies:

Pacini's and Ruffini's corpuscles. The former, already discovered by Vater, were described in detail by Pacini (1840), who saw them

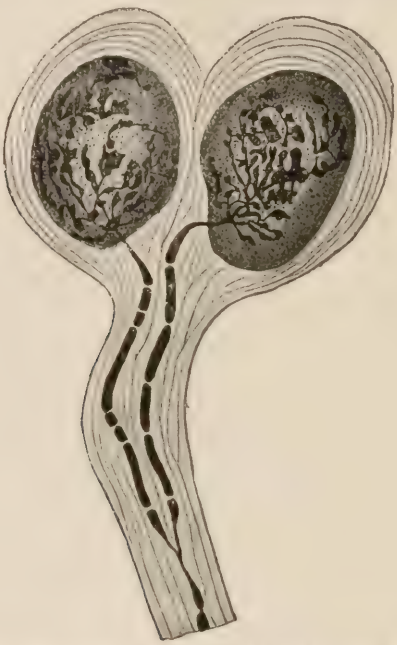


Fig. 10.—Two Golgi-Mazzoni corpuscles connected with a single bifurcated nerve-fibre. (Ruffini.) The ramified fibres within the corpuscles present numerous varicosities, varying in size and appearance.

adhering to the branches of the nerves that run in the fat under the skin of the palm of the hand and sole of the foot, as small oval

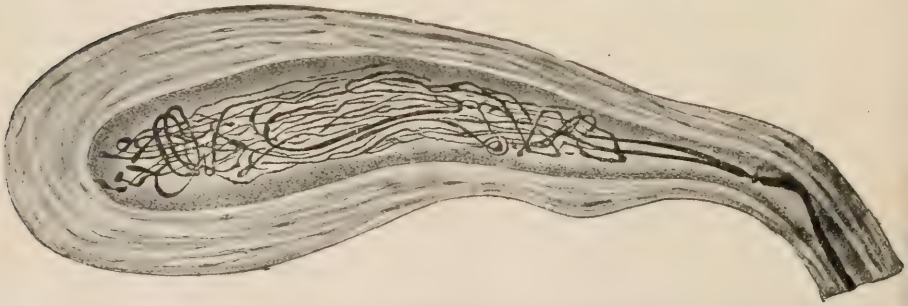


Fig. 11.—Variety of Golgi-Mazzoni corpuscle, distinct from the preceding because the non-myelinated nerve-fibre forms a characteristic interlacement in the core. (Crevatin.)

bulbs, quite visible to the naked eye (Fig. 13). They are too well known to require further description. As is well shown in Fig. 14, the Pacinian corpuscle consists of a capsule of finely lamel-

lated tissue and a central core penetrated by the medullated fibre, which runs through it direct to the end, where it branches and ends in an enlargement.

Between the largest Pacinian corpuscles, that are plainly visible to the naked eye, and those of Golgi-Mazzoni, which can only be detected with the microscope, there is an uninterrupted series of intermediate or transitional forms. One very rare variety of Pacinian corpuscle found in subcutaneous tissue consists of small spherical corpuscles with an inner core which is also spherical, and nerve-endings represented by a cluster of bulbs (Fig. 15).



FIG. 12.—Golgi-Mazzoni corpuscle. (Crevatin.) Besides the myelinated nerve-fibre, a fine non-myelinated fibre penetrates into the corpuscle and forms a network in the capsule, as described by Timofeew.



FIG. 13.—Nerve of middle finger with Pacinian corpuscles. Natural size. (Henle and Kölliker.)

The corpuscles which Ruffini discovered in 1891 have in common with Pacini's that they are found in approximately equal numbers in subcutaneous cellular tissue, and like the Pacinian bodies are of very variable dimensions. They are cylindrical and spindle-shaped. A capsule consisting of a few thin lamellae closely applied together can be distinguished from a supporting bundle of fibrillary connective tissue and elastic fibres, between which the nerve-fibres penetrate and expand in the form of a non-myelinated ramification. Sometimes the nerve-fibres enter laterally (Fig. 16); at other times they enter at one end of the spindle (Fig. 17).

Ruffini's corpuscles also present many variations. The

cutaneous nerve-plates of Crevatin, and the arboriferous terminations of Dogiel, have been described under this name, but differ in certain very important morphological characters.

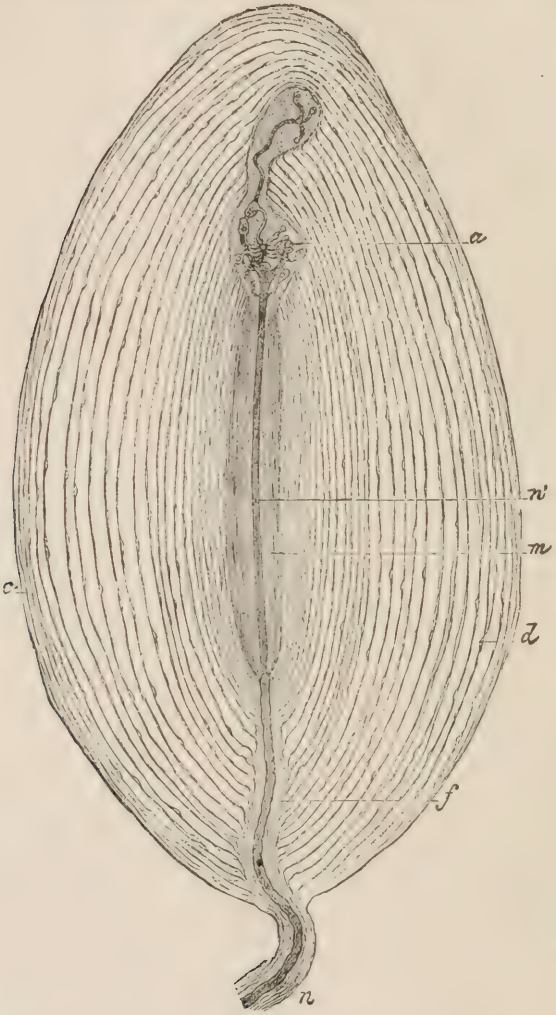


FIG. 14.—Pacinian body, from cat's mesentery. Magnified. (Ranvier.) *n*, Peduncle, with nerve-fibre enclosed in sheath of Henle passing to the corpuscle; *n'*, *m*, its continuation after loss of sheath; *a*, branched nerve-ending at the distal end of the core; *d*, lines separating the tunics of the corpuscle; *f*, channel through the tunics traversed by the nerve-fibre; *c*, external tunics of corpuscle.

All these end-bulbs are found more abundantly on the parts of the skin that are free of hairs, particularly such as habitually serve as tactile surfaces. Over the whole of the rest of the skin

where there are hairs, representing, according to v. Frey, about 95 per cent of the total cutaneous area, the various corpuscles we have referred to are not absent, but become less frequent, and are further apart in proportion as cutaneous sensibility in its different forms is less acute. To compensate for this the hairy parts of the skin contain a specially important form of nerve-ending, which is absent in other regions—this is the nerve-plexus, which can be seen round the hair follicles beneath the mouth of the sebaceous glands. Arnstein (1876) with the gold chloride method first successfully demonstrated the nerve-endings around ordinary hairs. He saw that after reaching the hair-follicle the medullated fibres lose their medullary sheath, divide, and give rise to a series of annular and longitudinal fibrils. The latter



FIG. 15.—Rare variety of Pacinian corpuscle. (Ruffini and Stameni.)

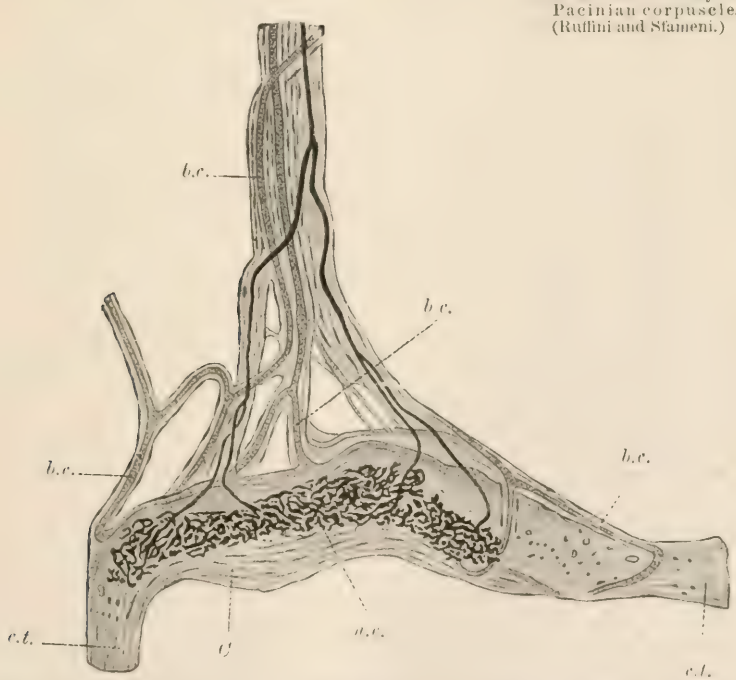


FIG. 16.—Ruffini's corpuscle, showing nerve-fibres entering from the side. (Ruffini.) *b.c.*, blood capillaries; *n.e.*, nerve endings; *C.*, capsule; *c.t.*, connective tissue.

are highly varicose and more external; they rise along the hyaline layer towards the surface of the skin, and terminate in wide disc-

like enlargements (Fig. 18). The nerves of human hair have not



FIG. 17.—Ruffini's corpuscle, in which the fibres penetrate into one end of the spindle. (Ruffini.) *C.*, Capsule; *H.*, sheath of Henle; *s.t.*, sustentacular tissue; *n.e.*, nerve-ending.

yet been described and studied: but everything leads us to conclude that they are similar to those of the hairs of other mammals.

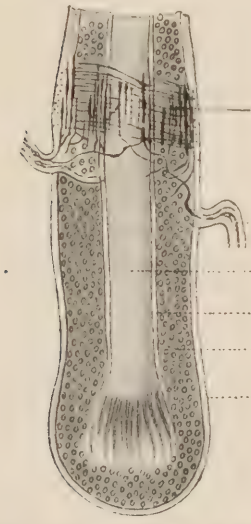


FIG. 18.—Section through a hair and hair sheath of cat magnified 160 times. (Böhm.) *pl.*, Nerve plexus; *N.*, nerve; *H.*, hair; *t.i.*, tunica interna of root of hair; *t.e.*, tunica externa; *h.l.*, hyaline layer.

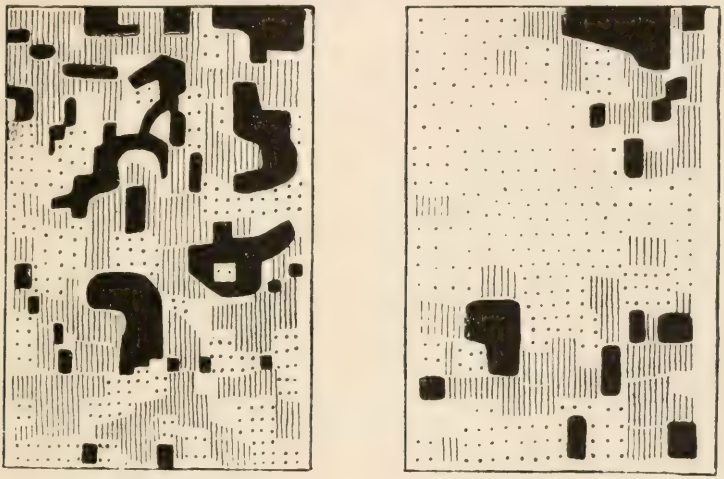
As regards the specific sensory function of the several forms of cutaneous nerve-endings, it must be confessed that our knowledge has made little progress. The peripheral organs for appreciation of pressure are undoubtedly represented in all parts of the skin provided with hairs by the above-described nerve-plexus in the outer sheath of the hair-root. Blix, and more recently v. Frey, have demonstrated that a pressure point corresponding with each hair lies near the point at which it emerges, on that side from which the hair follicle slopes.

In regions that have no hairs it can be affirmed with great probability that Meissner's corpuscles correspond to the pressure points. The results of Blix and v. Frey in fact agree with the old view on which Meissner's corpuscles were always held to be tactile.

Their superficial position in the skin corresponds to the sharp demarcation of tactile points, to their accessibility, unlike the nerve-plexus of the hairs, to electrical stimuli, and

to the fact that appreciation of pressure is lost in cutaneous scars.

Von Frey also suggested with much probability that the pain spots, which are most abundant in the skin, are served by the free terminations of the superficial nerve-plexus, which supply the epithelium of the Malpighian layer. It is possible that each pain spot corresponds not with a single nerve-ending but rather with a group of nerve-endings, otherwise the pain spots found by v. Frey in certain regions would have to be much more numerous and closer together. The fact that the cornea, which v. Frey found to be destitute of any specific sensibility except pain, is



A B

FIG. 19.—Topography of areas sensitive to cold (A), and to warmth (B), on same part of the anterior surface of the thigh. (Goldscheider.) The black areas are highly sensitive to thermal stimuli; the striated areas moderately so; the dotted areas very slightly; the spaces left white are not at all sensitive to such stimuli.

provided with a nerve-plexus that has free infra-epithelial endings, as described by Cohnheim (1866), supports this conclusion. Similar nerve-endings have also been recently described in epithelium which is not ectodermal in origin, and in the interior of many tissues—which increases the probability that they are related to pain sensibility, as this, when very slight, is allied to a sensation of tension or of simple contact, as Nagel (1895), in opposition to v. Frey's view, observed in the cornea.

It is far less easy to identify the peripheral organs that subserve the sensations of heat and cold. By elimination it may be said that Dogiel's corpuscles, Ruffini's papillary endings, and the Golgi-Mazzoni corpuscles are the organs for the sensation of cold, while Pacini's and Ruffini's corpuscles function, at least in the skin, as organs for the sensation of heat. The fact that the

latter lie in the deepest layer of the skin agrees well with v. Frey's statement that the heat spots are the most difficult to determine and have a longer reaction time. On the other hand, it appears probable from an interesting observation by v. Frey that the sensation of cold is dependent on the end-bulbs described by Golgi and Mazzoni. The conjunctiva of the eye is insensitive to pressure and heat, while its sensitiveness to cold, on the contrary, is very definite: Dogiel's observations show that the end-bulbs are abundant in the conjunctiva.

VI. Although the sensations of heat and of cold represent two modalities which depend on distinct sense-organs they may conveniently be discussed together, as most of the observations on this subject gain in interest by comparison.

Sensibility to cold and heat not merely includes the external cutaneous surface, but also extends to the skin of the auditory canal, and the mucous membrane of the nose, mouth, pharynx, and anus. The conjunctiva of the eye and external mucous membrane of the genital organs are insensitive to heat, but sensitive to cold. The rest of the mucous membrane, *e.g.* in stomach, intestine, etc., is totally destitute of any thermal sensibility—as E. H. Weber showed in 1851.

We saw that it is easy by means of punctiform stimulation to demonstrate that the two thermal senses are unequally distributed in the different cutaneous regions, and that cold spots are much more numerous than heat spots.

Goldscheider, in order approximately to map out the distribution of thermal sensibility, experimented on different cutaneous regions with thermo-aesthesiometers in the form of metal cylinders, 3-4 mm. in diameter. With this method it is possible to excite a greater or less number of thermal points by heat and cold. If the skin-surface investigated contains no thermal point, it has no thermal sensibility, and its thermal sensibility varies according as it contains many or few thermal points for heat or cold. It must be noted, however, that the degree of sensibility is not proportional to the number of excited sensory points, because the excitability of the latter has been experimentally proved to vary considerably: the presence of a few highly excitable points may make one area of the skin appear more sensitive than another which contains more thermal points that are less excitable. Goldscheider's method does not therefore determine the greater or less abundance of thermal points in different parts of the skin, but merely the mode in which these react to ordinary stimulation by heat and cold.

Figs. 19 and 20 from Goldscheider's memoir illustrate the results obtained by this method. They show that the sensibility to heat is invariably less developed both in intensity and in extent than that to cold. According to Goldscheider there is no

region in which sensibility to warmth is more developed than that to cold. This holds good both for the covered and for the uncovered regions. Where the sensibility to heat is highly developed, that to cold still preponderates, both in intensity and in extent. There are—as we have said—regions in which sensibility to cold is more or less acute while sensibility to warmth is very low or entirely absent.

The varying thermal sensibility in different cutaneous areas depends not only on the greater or less abundance of cutaneous nerves, but also on the varying thickness of epidermis that covers the nerve-endings, and also perhaps on the depth at which the nerve-endings themselves are situated.

Previous to the discovery of the duality of thermal sensation

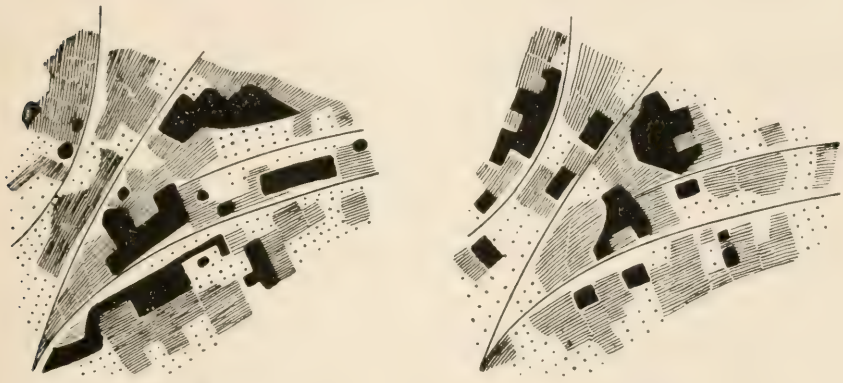


FIG. 20.—Topography of sensibility to cold (A), and to heat (B), in same part of palm of left hand. (Goldscheider.) Explanation in previous figure.

Weber and Nothnagel attempted to map out thermal sensibility by exploring certain regions of the skin with flasks of oil, or with the rounded ends of large keys previously cooled or heated. After the discovery of heat and cold spots, Goldscheider (1887) extended the research by using metal cylinders, at a temperature of 15° for cold and 45°-49° for heat. More recently Veress (1902) has again investigated sensibility to heat on himself by means of his thermo-aesthesiometer (Fig. 1, p. 14). Here we can only cite the most conclusive of his general results:—

(*a*) Sensibility to heat is not equal in the two halves of the body. On an average it is rather greater on the left than on the right.

(*b*) The most mesial parts of the trunk are, generally speaking, less sensitive to heat than the lateral regions.

(*c*) The trunk is, generally speaking, more sensitive to heat than the extremities.

(*d*) Sensibility to heat is not uniform in the extremities; some distant parts are more sensitive than others more proximal.

(*e*) The lateral surfaces of the extremities are less sensitive to heat than the mesial sides.

To these conclusions we may add that in those cutaneous regions which are peculiarly adapted to tactile sensibility (as the hand in general, the tips of the fingers in particular) the thermal sensibility to both the cold and heat sense is less than in other regions.

Parts that are habitually covered are more sensitive to cold than exposed parts. This is not due entirely to habit, but principally to the fact that the covered parts contain a great many cold spots: for the same reason the skin of the face, though it is constantly exposed, is not less sensitive to cold than the covered parts of the skin.

The terminal apparatus of the thermal nerves has in common with other nervous organs the property of being more strongly excited in proportion as the stimulation is more rapid. As the adequate stimulus consists in the addition or subtraction of heat at the thermal points, it may be said that the excitation or reaction of the latter is more intense in proportion as the increment or decrement of heat occurs more rapidly.

The strength of the sensation also depends partly upon the extent of cutaneous surface excited. A thermal stimulus distributed over a large area of skin evokes a stronger sensation than a stimulus of the same strength acting on a smaller area. This is easily demonstrated by plunging one finger of one hand and the whole of the other hand into water; or by dipping one finger into water at 40° C. and the other hand into water at 37° C. In both experiments the sensation of warmth is less in the finger than in the hand. Weber also noted that a stimulus which is purely thermal when applied to a small surface may become painful if it acts on a larger surface. One finger alone can be plunged into water at a temperature at which the immersion of the whole limb would be painful.

The reaction time for sensations of cold and that for tactile sensations are equally short; on the other hand, the reaction time for sensations of heat, as that for sensations of pain, is longer (Tanzi). According to Kiesow and Ponzo, the reaction time for heat is shortened if stimuli that penetrate the skin more readily than those employed by Tanzi are adopted, and if the specific points are excited directly. Nevertheless, it still remains longer than that for sensations of cold and contact. According to Kiesow's latest work, the reaction time to pain sensations is much shortened if sharp-pointed stimuli are used. From this it results that if one and the same cutaneous region is excited simultaneously with cold and hot stimuli, the sensation of cold

precedes that of heat. Further, the excitation of any spot by cold produces a more lively sensation, that reaches its maximum more rapidly than excitation of the same spot by heat. According to v. Frey this difference is not apparent on exciting the two thermal spots by electrical stimuli. From this he concluded that the nerve-organs of the warm spots lie in the deeper layers of the skin, and those of the cold spots in the more superficial layers.

The physical properties of the thermal agents, again, have an influence on the effects of excitation. Stimuli may consist of solid, liquid, or gaseous bodies, and may act by conducting heat or by irradiation; they may be good or bad thermal conductors; their thermal capacity may be large or small; lastly, they may have a smooth or a rough surface.

Thermal sensations are stronger according as the stimulating body is a good conductor of heat. Water at 25° C. is a stronger stimulus of cold than oil, and less strong than mercury at the same temperature. It is possible to arrange a graduated series of bodies with different thermal conductivities, but all of the same temperature, by which a series of thermal sensations of gradually increasing strength can be excited. This, however, applies only to intensity of sensation as evoked by the initial contact. With prolonged contact new relations are set up, due to variations in the thermal exchanges between the cutaneous surface and the external agent, so that a first impression of cold may be translated into a sensation of warmth. For instance, on dressing, or lying down in bed undressed, the first sensation is one of cold, followed quickly by the opposite sensation of warmth, which may be less or greater according to the nature and thickness of the clothing or bed-covering.

Any body that serves as a thermal stimulus must, besides its power of conducting heat, also possess a certain minimal thermal equation in order to produce a sensation: the latter within certain limits may increase in intensity with an increasing thermal equation of the stimulating body. Thunberg has shown that various degrees of thermal excitation can be evoked in the skin by contact with bodies that have the same temperature but different thermal properties, for instance a series of silver or copper plates of various thicknesses. By means of these plates it is easy to determine the minimal degree of heat required to evoke a thermal sensation.

The importance of the smoothness or roughness of the surface of the body that is used as a thermal stimulus is easily understood, seeing that the conduction of heat, and hence the efficacy of stimulation, varies according as the points of contact between the skin and the conducting body are few or many.

The essential conditions for the production of sensations of heat or cold must consist in the thermal changes that take place

in the skin. So long as the temperature of any part of the skin remains constant between certain mean limits, there is no excitation; but as soon as the temperature of this region changes, either from external or internal reasons, thermal sensations at once arise.

Normally a slow, continuous thermal current flows through the skin from within, outwards. So long as the conditions of this current remain unchanged, the temperature of the nerve-organs remains the same; but if the current alters with a certain rapidity, there is a sensation of warmth or cold in consequence of the rise or fall of temperature in the end-organs. According to Weber it is these changes in the temperature of the end-organs which constitute the adequate stimulus and the essential conditions of thermal sensation, no matter what caused the alteration of temperature. It almost seems, he writes, as if we could detect the process of rise and fall in the temperature of our skin much better than the degree to which the temperature rises and falls. Since the discovery of specific organs for cold and heat, it has become possible to give a more exact definition to Weber's theory, by saying that the organs for cold are excited by fall of their temperature, and those for heat by its rise.

This theory gives a satisfactory explanation of many facts. We are aware of a sensation of cold both when the loss of heat through the skin increases, and when the peripheral blood-supply diminishes. We have a sensation of warmth both when the loss of heat by the skin is decreased in consequence of a rise in the temperature of the environment, and when the peripheral blood-supply increases. Accordingly, it is not the direction of the thermal heat current from within outwards, or from without inwards, nor the intensity of this current, which produces the thermal sensations, as assumed by Vierordt, but the changes in temperature at the thermal end-organ, no matter what process causes them.

One fact, however, seems at first sight to contradict Weber's theory. If a metal at 3° C. is applied for some time to any part of the skin, for instance the forehead, and then removed, there will for some 20 seconds be a sensation of cold in that part instead of heat, as would be the case if the skin were growing warmer. Fechner and Vierordt also noted that it is possible to feel a prolonged sensation of heat or cold without any change in the temperature of the environment. These facts led Hering to conclude that not only thermal changes, but the absolute degree of cutaneous temperature as well, may act as a stimulus of thermal end-organs.

When the temperature of the environment remains fairly constant we are not as a rule aware of any thermal sensation, although the different parts of the skin may have a very different

temperature, according as they are exposed or covered. The temperature that produces no thermal sensation is not at any definite point of the thermometric scale, but, according to Leegaard, seldom ranges over more than 0·5° C. This *indifferent temperature* alters not only in the different regions of the skin, but also in the same region at various times. For instance, on passing from a room in which no thermal sensation is felt into one that is hotter or colder there is an immediate sensation of heat or cold. But if the difference in the temperature of the two rooms is not very great a new equilibrium will soon be set up so that no thermal sensation is perceptible. The surrounding temperature may therefore vary between considerable limits without producing any persistent thermal sensation. It might be supposed that this adaptability depends upon variations in the blood-supply to the skin, which to a certain extent protects the peripheral thermal end-organs from the oscillations of temperature in the environment. Thunberg, however, pointed out that it can be observed on a hand previously rendered bloodless. The adaptation therefore depends on an alteration of the excitability of the peripheral thermal end-organs, which causes a displacement of the level of the *indifferent temperature* or *physiological zero-point* (Hering) of thermal sensibility.

Starting from this fact Hering maintains that any intrinsic temperature of the thermal organs above the physiological zero-point is perceived as heat, and any temperature below the zero-point as cold. The intensity of the sensation of heat or cold increases with the variation of the intrinsic temperature of the end-organ from the physiological zero. Any intrinsic temperature of the end-organ appreciated as heat causes an upward displacement of the zero-point: any temperature appreciated as cold, a downward displacement. All sensation of heat and cold ceases when, owing to the displacement of the zero-point, the latter coincides with the intrinsic temperature of the end-organ.

The existence of two distinct senses for heat and cold is not fundamentally irreconcilable with this theory of Hering. It may be assumed that a rise in the cutaneous temperature acts only upon the organs of heat, and a fall upon the organs of cold. But the so-called *paradoxical sensation of cold* cannot be explained either by Weber's or by Hering's theory. If a metal point warmed to 45°-50° C. is applied to a cold spot a sensation of cold is felt (Lehmann and v. Frey). The accuracy of this observation has been confirmed by many authors (Alrutz, Kiesow, Thunberg, Veress, Bader). All cold spots react by a sensation of cold when brought into contact with a warm point. When a thermo-aesthesiometer is applied over an extensive surface, cold spots are stimulated as well as heat spots, but the sensation of warmth

predominates and masks the opposite sensation of cold. Thunberg, however, by choosing an appropriate form of stimulus succeeded in producing the two sensations separately, first cold and then heat, which is a strong argument that the nerve-organs for cold lie in a more superficial layer of the skin than those for heat.

The paradoxical sensation of heat was first observed by Strümpell in anaesthesia produced by freezing, and was described under the name of "perverted thermal sensibility": Lerda (1905) encountered it in certain small cicatrices of not too recent date; Michael Sugar (1910) in a patient with syringomyelia and in a few cases of multiple sclerosis; Ponzo (1909) in areas of skin that had been artificially anaesthetised by means of subcutaneous injections of stovaine; Fontana (1912) in patients suffering with large condylomata.

VII. Sensations of pressure, like sensations of heat and cold, are elementary, and cannot be split up into simpler components. Pressure sensations enable us to appreciate the surface contact of external objects independent of their temperature.

Meissner believed it possible to distinguish sensations of *simple contact* from *pressure sensations*, as if they differed fundamentally. But later observations showed that both are due to deformation of the cutaneous surface, and therefore represent different degrees of a single quality of sensation. When the contact is so light that it produces no pressure on the cutaneous surface, there is no sensation of any kind.

The functional importance of the sense of contact or pressure lies in the fact that by its means we are able to perceive the slightest mechanical impact upon the surface of our bodies. Meissner's corpuscles and the nerve-rings that surround the sheath of the hairs are homologous organs that come into play during sensations of contact. They are capable of excitation by mechanical agents a thousand times weaker than those necessary for the direct excitation of the peripheral nerves (Tigerstedt).

We have already pointed out that the heat and cold points do not coincide with the points for contact or pressure. We may now add that the regions of maximal sensibility to thermal stimuli differ from those of sensibility to tactile stimuli.

An exact comparative determination of tactile or pressure sensibility in the different regions of the skin is very difficult. The pressure exerted by a gas or fluid is certainly the best means of exerting a uniform pressure upon every part of the curved surface of human skin. But we know from experience that such a pressure is not appreciable. We are quite unaware of the pressure exerted by the atmosphere upon the surface of the body as a whole, and of the hydrostatic pressure when the entire body is bathed in water. The physiological effect depends not only on the amount of pressure exerted on the skin, but also on

the number of superficial cutaneous elements on which the pressure acts. The effect seems to be greater or more easily perceived in indirect relation to the area of skin compressed. Von Frey's method of determining the tactile sensibility in different regions of the skin by *hairs* is based on this fundamental observation.

With this method it is easy to prove that the parts most sensitive to mechanical agents are the tip of the tongue, the red part of the lips, and the ends of the fingers. Even in these parts there is a threshold of stimulation which must be crossed to evoke a sensation. This shows that the parts where the sense of pressure is most delicate do not coincide with those in which thermal sensibility is most developed, which is a valid argument in favour of the theory that the two forms of sensation arise in different end-organs.

We know nothing about the nature of the process by which the excitation takes place. Possibly it may consist in a discharge of energy caused by a chemical change within the end-organ, due to a displacement of fluid—a change in the concentration of the dissolved substances—which acts as a chemical stimulus. We know that continuous pressure of a certain intensity on a sensory nerve produces a continuous sensation, which is difficult to explain as a mechanical effect, because the work required to stimulate an exposed nerve is probably a thousand times greater than that sufficient to excite those nerves adequately when it acts on their terminal end-organs. We have consequently no reason to reject the hypothesis that mechanical stimuli can only excite the nerve indirectly, and that excitation is always due to alteration of the chemical structure or to osmotic pressure of the tissue fluids (v. Frey and Kiesow). At the same time we cannot exclude another simpler though more indefinite hypothesis, according to which excitation depends upon a purely physical process, by which the mechanical stimulus is changed into another form of energy, to which Meissner's corpuscles are far more sensitive.

As regards the mode of action of a mechanical stimulus in producing sensations of contact and pressure, v. Frey and Kiesow (1899) showed that it is not compression in itself that determines the excitation, but the deformation of the skin surface, which produces an alteration in the pressure (*Druckgefälle*), and this again indirectly produces an active reaction of the terminal organ. This alteration is produced both by compressing the skin with a point or small surface, and by pulling on a small body or disc attached to the surface of the skin. In the first case the pressure is greatest at the compressed surface, and diminishes in the deeper parts and in the surrounding areas of the skin; in the second the pressure is least in the part of the skin drawn up, and increases

towards the deeper parts and in the surrounding areas (Fig. 21). Both the positive and the negative alterations give rise to sensations of contact, and this with approximately equal strength of stimulus shows the same characteristics on compression and on traction. Accordingly the excitation of the sense-organ of pressure is due to alteration in the intrinsic pressure of the organ, and the intensity of the sensation depends on the amount and not on the direction of the alteration.

Since it is not possible to measure exactly the alteration in pressure which, with different means of mechanical excitation of the skin, gives rise to the sensation of pressure, it follows that in order to obtain even an approximate valuation of the effective threshold of stimulation we must take into account all the factors that may raise or depress it. The investigations of v. Frey and Kiesow show that the liminal value varies with the rate of

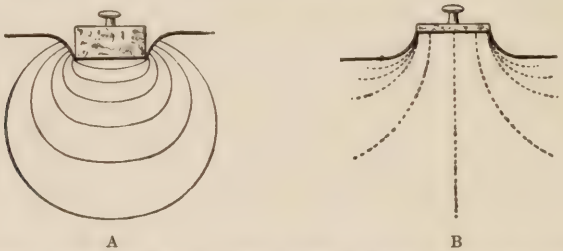


FIG. 21.—Diagram of deformation of a cutaneous area (shown in section) by compression with a weight (A), and by traction on a disc previously attached to the skin (B). The continuous curved lines in A represent the positive change of pressure; the dotted lines in B represent its negative change. The variations of pressure in the skin are maximal at the edges of the weight or disc, and become gradually less below the area compressed or pulled upon.

stimulation and with the nature, size, and depth of the cutaneous deformation. As regards the manner in which the mechanical stimuli may at least be appreciated relatively if not measured exactly, they concluded that :—

(*a*) The liminal mechanical stimulus cannot be estimated by weight, because the effect of a given weight always depends on the area of the surface of contact.

(*b*) When the surface of contact remains constant, a given weight produces a different effect on different parts of the skin, because the number and the sensibility of the nerve-endings excited varies in different cutaneous areas. It is consequently only possible to compare liminal estimations when the experiment is confined to the excitation of single nerve-endings, *i.e.* to single tactile spots, by means of v. Frey's hairs.

(*c*) If the same tactile spot is stimulated by a weight which has a constant surface of contact, so as to produce near any such point a deformation constant in depth and surface, the effect of such an excitation varies with the rate at which the deformation

takes place. A deformation rapidly produced has more effect than one produced slowly. It follows that the effect of the stimulus is not dependent on the mechanical work performed, because different amounts of mechanical work may produce identical sensations, and *vice versa*.

(*d*) If on stimulating one and the same tactile spot the surface area of the stimulus is altered, then to obtain approximately the same effect the weight and rapidity of stimulation must be correspondingly altered. Hence the results obtained with different methods can only be compared when the increment of weight for the unit of time and surface, *i.e.* the rate of pressure, remains constant.

The results which v. Frey and Kiesow obtained on exciting large and moderate cutaneous areas show that the threshold values of the weights do not increase in proportion with the increase of the surface deformed. This can only be explained on the theory that the excitation which causes a sensation of pressure depends on the alteration in pressure produced within the skin, and that any pressure that is *equal on all sides* produces no effect at all. As the excited surface grows larger the fall of pressure in the skin becomes less. On the other hand, the smaller the stimulating surface, the more rapid will be the alteration in pressure; an increase in surface pressure then becomes necessary to produce a change in pressure at the level of the nerve-organ adequate to excite it.

On the strength of these investigations it is easy to explain the well-known experiment of Meissner. If the hand is dipped into a fluid—water or mercury—of the same temperature as the hand a pressure sensation is not felt over the whole surface of the submerged skin, but only at the boundary between the parts compressed and those not compressed. If, *e.g.*, one finger is dipped into mercury at the same temperature as the finger, a sensation is felt of a ring compressing the finger. This sensation is referred to the level at which there is an alteration in the pressure, while there is no sensation over the whole surface that is exposed to a gradual and slowly increasing pressure, since the variation is so slight that it remains below the effective threshold of stimulation.

Kiesow (1904), in a long series of patient and delicate researches by the most modern methods, attempted to estimate as accurately as possible how the sensibility to touch and pressure alters upon the different parts of the surface of the body. He investigated in two directions. He determined separately the number of the touch spots (or pressure spots of Blix and Goldscheider) in the surface unit, and then the liminal stimulus for the touch spot, that is the mean value of the threshold, obtained by a series of separate observations in different cutaneous regions. These estimations were made by means of v. Frey's hairs.

The results of these researches were published by Kiesow in a number of tables, of which we can only cite the final conclusions. In these Kiesow compared the relative sensibility of the different cutaneous areas which he examined (arranged in order of increasing sensibility), according to the mean liminal values obtained and to the number of the touch spots per surface unit.

Kiesow started from the region in which sensibility to contact or pressure is lowest, which he designates as 1, and on comparing all the other regions to this, obtained the following results for their *mean* liminal values :—

Back, median line, level of 3rd dorsal vertebra	1·00
Abdomen, white line, midway between umbilicus and pubic symphysis	1·06
Thorax, median line, level of 5th intercostal space	1·24
Thorax, left axillary line, level of 5th intercostal space	1·33
Thorax, median line, level of 4th intercostal space	1·39
Thorax, left axillary line, midway between xiphoid and umbilicus	1·79
Left patella, middle of	1·95
Left leg, in the middle of the anterior surface	1·99
Back, median line, level of antero-superior iliac spine	2·23
Left thigh, anterior surface, about 1 cm. from edge of patella	2·31
Back, median line, level of 7th cervical vertebra	2·72
Thorax, median line, level of 2nd intercostal space	2·77
Left leg, calf	2·96
Left arm, middle of flexor surface	3·01
Left wrist, stiloid process of ulna	3·05
Left elbow	3·09
Left forearm, upper part of flexor surface	3·12
Left wrist, dorsal surface, middle line	3·26
Dorsum of left foot	3·38
Left wrist, radial surface	3·49
Left forearm, middle of flexor surface	3·80
Wrist, 2·7 cm. above the joint	3·80
Left upper eyelid	7·16
Forehead (glabella)	7·54

For the tip of the tongue, red part of lips, and tips of fingers, Kiesow, starting from the same value of 1, and taking the *minimal* liminal values (not the *mean*, as above), obtained the following results :—

Finger-tips of left hand	3
Edge of lower lip, middle part	50
Tip of tongue	60

Kiesow obtained the following number of touch spots in the surface unit (1 sq. cm.), starting from the region in which they are fewest (= 1) :—

Leg, middle of anterior surface	1·00
Calf	1·16
Left patella, middle	1·60
Left forearm, middle of flexor surface	1·85
Left arm, upper part of flexor surface	2·00
Left elbow	2·43

Left thigh, anterior surface, about 1 cm. from edge of patella	2·87
Back, middle line, level of ant. sup. iliac spine	3·13
Left forearm, middle of flexor surface	3·22
Thorax, left axillary line between xiphoid process and umbilicus	3·25
Thorax, middle line, level of 2nd intercostal space	3·85
Left wrist, stiloid process of ulna	4·10
Thorax, middle of axillary line, level of 5th intercostal space	4·15
Thorax, middle line, level of 4th intercostal space	4·35
Dorsum of left foot, middle	4·75
Back, middle line, level of 3rd dorsal vertebra	4·75
Thorax, middle line, level of 5th intercostal space	4·95
Left wrist, radial surface	5·15
Left wrist, dorsal surface, middle line	5·60
Left wrist, flexor surface, 2·7 cm. from the fold	5·70
Back, level of 7th cervical vertebra	6·35

Comparison of these tables shows that the two factors on which the pressure sensibility in the different regions of the skin depends (the *mean liminal value* and the *number of tactile points* in the surface unit) are more or less compensatory, but partly correspond. In other words, in certain cutaneous regions the infrequency of points is compensated up to a certain point by the lower effective liminal stimulus, or conversely, the higher liminal excitation is partly compensated by a comparatively greater abundance of touch spots; in other regions, on the contrary, both the mean liminal value and the number of tactile organs contribute in raising or lowering the local sensibility to contact or pressure.

If the results which Kiesow obtained for the number of touch spots in the surface unit are compared with those previously worked out by Goldscheider and Blix, it is found that they are, on an average, intermediate between those of Goldscheider, which are excessive, and of Blix, which are too low. This depends partly on the difference in the methods adopted by the three workers. Alrutz (1905) controlled Kiesow's results, replacing v. Frey's excitatory hair by a glass thread, which he preferred because it is not affected by damp; also a hair is never straight and its elasticity alters with use. His results are in entire agreement with Kiesow.

It is an interesting fact that Kiesow's results on the topographical variations in sensibility to pressure agree surprisingly with those obtained by Weber's classical investigations with the compass, which we shall presently discuss.

Weber's observation showed that cold objects, such as coins, placed on the skin are estimated to be heavier than warm objects of the same weight and size. Kiesow showed that this depends on the fact that cold produces a positive change of pressure in the skin, in a manner analogous to a compressing mechanical stimulus: heat, on the contrary, like traction, causes a negative change in the pressure (Fig. 21). So that there is in the first case

an increase, in the second a decrease, of the action set up by the mechanical stimulus within the skin.

VIII. When any part of the skin is excited by a small surface or a blunt point, we are able, even with the eyes shut, to indicate more or less exactly the place of excitation. Weber termed this capacity of localising cutaneous excitation the "sense of locality"; others have termed it the "spatial sense." These terms are ill chosen, as they suggest that there is a specific localising sense in the skin, other than those of contact or pressure, and of heat and cold, to which our sensations of locality or space must be referred. In reality, these sensations are only the perceptual signs of the cutaneous sensations which have already been discussed; in other words, we perceive not only contacts, and positive or negative changes in temperature, but also their seat, that is the area or surface of the skin that is altered by tactile and thermal stimuli.

There are two methods of determining cutaneous localisation, both of which were employed by Weber:—

(*a*) The skin of a blindfolded subject is touched with a blunt point, and the subject must at once indicate the spot touched. The degree of error is measured in millimetres and indicates the degree in which the region is sensitive to localisation.

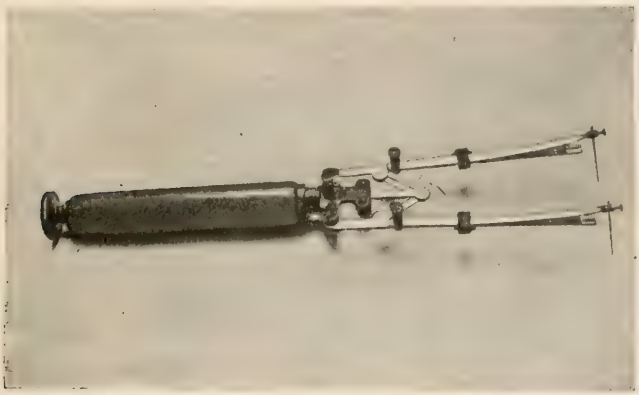
(*b*) The blunt ends of a compass or other instrument with a scale (Fig. 22—aesthesiometer of Weber, v. Frey, Giesbach, Binet, Ponzo, and others) are applied lightly and simultaneously to the skin. The blindfolded subject has to say if two separate contacts are perceived, or only one. The power of localisation in the region under examination is measured by the minimal distance at which the two points of the compass are perceived separately, and not as a single contact.

According to Vierordt the delicacy of tactile spatial perception seems at many points of the body-surface to be in a certain relation with their mobility, in so far as it corresponds to the variety and rapidity, direction and range of the movement. Spatial discrimination is maximal at the tip of the tongue, which is able to move rapidly in all directions. In the skin of the limbs it increases from the proximal towards the distal regions, and is greatest at the finger-tips, the most distal segments, where the range of movements of the limb is maximal; these are also the parts usually employed as tactile organs.

Both in the skin of the limbs and that of the trunk tactile discrimination is more developed in the transverse than in the longitudinal axis, and on the flexor surfaces than on the extensor surfaces (Weber); in the intercostal spaces the errors are mainly in the direction of these spaces, from which it appears that the direction of the nerves has some influence upon the direction of errors in localisation (Ponzo).

In young people tactile discrimination is better developed

than in adults, because the touch spots lie closer together (Landois). It varies considerably with different individuals even within physiological limits; numerous observations show that it can be developed and improved by practice. Czermak and Gartner found that the power of localisation is more highly developed in the blind than in normal people, and Volkmann noted that the improvement takes place on both sides of the body, although the sense of touch is nearly always better appreciated by the right hand. One of the most striking proofs that tactile discrimination is improved by practice is that in compositors it is extraordinarily well developed in the fingertips. In the highly mobile parts of the limbs, a few hours of practice are enough to increase tactile discrimination to a



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FIG. 22.—Ponzo's new aesthesiometer, substituted for Weber's compass, consists in a handle and two arms that can be adjusted by means of a screw at the end of the handle. The arms carry two brass clips with two points at their ends. To vary the quality of the tactile, thermal, or painful stimulus the blunt ivory points may be replaced by blunt or sharp metal points.

remarkable degree, almost to double it. In the immobile and more protected regions, on the contrary (*e.g.* the skin of the trunk where it is low), even prolonged exercises do not increase it perceptibly. It is certain that education of any area of the skin on one side increases sensibility, not only in the vicinity of that area, but also in the corresponding area of the opposite side.

Many conditions alter the delicacy of tactile localisation. If a limb is raised so as to make it anaemic, or the veins are compressed till there is congestion or venous stasis, spatial sensibility is blunted. The same occurs when the attention is fatigued by unduly protracted tests (Alsberg), and by the action of cold (Goltz); after prolonged application of the anode of a galvanic current (Spanke); on passive distension of the skin (Czermak); by certain poisons—atropine, daturine, morphine, strychnine, cannabine, alcohol, chloral hydrate, potassium bromide (Sichtenfels and others).

According to Sherrington, cerebral cortical lesions in man disturb tactile localisation far more than any other form of cutaneous sensibility; the patient, in fact, may refer a touch on the hand to the forearm.

Before discussing the results obtained by various experimenters on the sense of localisation in different regions, it is necessary to point out certain facts that must be remembered in using Weber's aesthesiometer. These are:—

(*a*) If the two ends of the compass are put down one after the other, instead of simultaneously, the two contacts will be appreciated at a less distance.

(*b*) The same occurs if, in estimating the liminal distance at which the compass-ends are separately perceived, the alteration is made from greater to less distances between the points, instead of from less to greater.

(*c*) If one of the ends is warmer or colder than the skin the two contacts will be perceived at a less distance than if both points are of the same temperature as the skin.

(*d*) Bathing the skin with indifferent fluids increases tactile discrimination, *i.e.* the discrimination is sharpened.

(*e*) If the skin is gently stroked between the two ends of the compass, or electrified with weak currents, one end only will be detected, where both had previously been perceived.

The following table gives the value in millimetres of the mean liminal distances for perception of the two points of the aesthesiometer, obtained by Weber on a normal adult subject, and by Landois on an intelligent boy of 12 years old.

	Adult.	Boy.
Tip of tongue	1·1	1·1
Palmar surface of third phalanx	2·2	1·7
Red part of lips	4·5	3·9
Palmar surface of second phalanx	5	3·9
Palmar side of first phalanx	5	...
Dorsal side of third phalanx	6·8	4·5
Tip of nose	6·8	4·5
Ball of thumb	7	...
Middle of palm	8·9	...
Middle of dorsum and edge of tongue	9	6·8
Metacarpus of thumb	9	6·8
Plantar surface of third phalanx of big toe	11·3	6·8
Dorsal surface of second phalanx	11·3	9
Cheek	11·3	9
Eyelids	11·3	9
Centre of hard palate	13·5	11·3
Palmar side of lower third forearm	15·0	...
Anterior part of zygomatic region	15·8	11·3
Plantar side of metacarpus of big toe	15·8	9
Dorsal surface of first phalanx	15·8	9
Dorsal head of metacarpus	18	13·5
Inner part of lips	20·3	13·5
Posterior part of zygomatic region	22·6	20·3

	Adult.	Boy.
Lower occipital region	27·1	22·6
Dorsum of hand	31·6	22·6
Chin	33·8	22·6
Vertex of head	33·8	22·6
Knee-joint	36·1	31·6
Sacral and gluteal regions	40·6	33·8
Forearm and leg	40·6	36·1
Dorsum of foot near toes	40·6	36·1
Sternum	45·1	33·8
Neck, high up	54·1	36·1
Dorsal spine, lower thoracic and lumbar region	...	54·1
Middle of neck	67·7	...
Middle of arm, thigh, back	67·7	40·6

Weber gave the name of *tactile circle* to the area within which the two points of the aesthesiometer are appreciated as a single point. If in any cutaneous area the localisation is equally developed in all directions, the circles are round, *i.e.* they approximate to the figure of a true geometrical circle; but this is very seldom the case. More often, particularly in the extremities, they are oval, because tactile discrimination is, as we have seen, more developed in the transverse than in the longitudinal direction. For this reason Hermann prefers the term *tactile fields* to *tactile circles.*

These tactile circles or fields have no fixed anatomical limits, and do not correspond to the peripheral distribution of a single nerve-fibre. If they did there would be a sudden transition from a single perception (when the two points were applied within one circle) to a double one (when the equidistant points were applied to two adjacent circles), which is not the case, since each point of the skin may be taken as the centre of a circle. As, moreover, discriminative sensibility differs enormously in different regions of the skin, as shown by the above table, this assumption is obviously irreconcilable with such a varying peripheral distribution of the sensory cutaneous fibres in the different parts. Weber accordingly assumed that each tactile circle contains many nerve-endings, and that for the recognition of the two contacts it is necessary that there should be between the two excited nerve-endings a certain number of unexcited end-organs, which vary in different regions according to their congenital arrangement. This theory is obviously less an explanation than a simple statement of fact. It does not explain how the tactile fields can be diminished by practice.

From the psychological point of view Lotze supposed that each nerve-fibre distributed to the skin or adjacent mucous membranes is provided in the brain with a *local sign* of recognition of the place to which it is distributed in the periphery. In developing this idea Wundt concluded that on stimulation each cutaneous area transmits to the brain not only the impression of

contact but also the sign of the place at which it occurs, which he calls *local colour*, to be used in consciousness as a *local sign*. The local colour of the excitations aroused in the skin is gradually differentiated as between one place and another by phylogenesis and by exercise. So long as the difference is slight it is not perceived in consciousness, and the two simultaneous impressions from adjacent points of the skin may fuse into one. But when the difference in local colour increases, because the two impressions arise from more widely separated points, both are appreciated. With exercise and attention it becomes possible to perceive differences in local colour that are not habitually noticed. This explains why the sensory cutaneous areas may be educated by practice.

This hypothesis is not a scientific explanation; it merely substitutes metaphor for fact, with a view to making it more acceptable. On the other hand, it is open to a grave objection: what has been said above shows that recognition of the place from which a sensation of contact arises is a function of the perceptive centre, and depends, as Johannes Müller showed and as is confirmed by later researches, on its *specific energy*. The nerves merely transmit an excitation or nervous vibration which is common to all the sensations; they do not transmit any quality, colour, or sign of recognition from the part touched.

Bernstein formulated an ingenious hypothesis to account for the phenomena observed on applying Weber's compasses to the skin. He held that when the excitation aroused in the skin by contact reaches the cortical centre it spreads more or less widely, as occurs in the periphery with sensations of pain. On the neurone theory this central spread of excitations coming from the periphery is a natural consequence of the fact assumed by Ramon y Cajal that each sensory fibre terminates at the centre in an arborescence; but even on Golgi's theory of the diffuse fibrillary network, which serves as a vehicle of central communication, it may be admitted that nervous activity spreads more or less widely through the meshes of the network according to the intensity of the stimulus. When two adjacent points of the cutaneous surface are touched, the two excitations on reaching the central surface spread and summate into a single excitation, which culminates in a point equidistant from the points of arrival from the two fibres (or groups of fibres) stimulated. In this case, therefore, there is only a single sensation of contact. When, on the contrary, the two points of contact are farther apart, the two excitations on reaching the centre do not summate, but two distinct apices are formed, which correspond with the points of arrival of the stimuli from the two fibres (or groups of fibres) stimulated. In this case, therefore, both contacts are distinctly perceived. Bernstein's theory is clearly illustrated by the geometric diagram (Fig. 23).

The lines *pp* represent the cutaneous surface, *CC* the central surface, in which are the central stations of the nerve-fibres *nn*. When point 1 on the skin is touched, the excitation is conducted to the corresponding point 1 in the cortex. The intensity of the excitation is expressed by the ordinate *ab*, and the curve *bcd* represents the spread of the excitation from the point of arrival (which corresponds with the apex) to surrounding points. The same phenomena occur when point 2 is touched separately; the curve *fgh* represents the spread of the excitation when it reaches the centre. Since points 1 and 2 lie in the same cutaneous tactile circle, there is a single sensation of contact when they are excited simultaneously. On Bernstein's theory this is because the two excitations represented by the two curves *bcd*, *fgh* summate

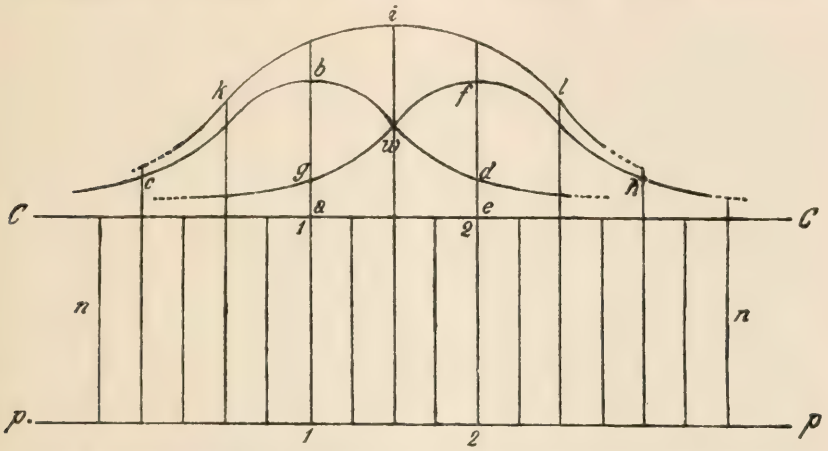


FIG. 23.—Diagram to show how excitations from two points on the skin summate at the centre into a single sensation. Explanation in text.

geometrically, and form a single resulting curve *ikl*, the apex *i* of which is at a point equidistant from the two component apices *bf*. When the distance between the two cutaneous points touched is increased, the two curves intersect at a point *w*, which becomes increasingly lower till they no longer cross; the two stimuli are then perceived separately.

While undoubtedly ingenious, this theory has weak points. Why do exercise and attention restrict the tactile circles? On what does the enormous difference between the area of the tactile circles in the more sensitive and the less sensitive regions depend? And even admitting that the theory explains why the two points of the aesthesiometer produce a single sensation within the limits of any circle, while beyond this circle two separate sensations are perceived, on what does our power of localising these sensations at the periphery depend?

In reply to the first question, Bernstein assumes that functional exercise increases central resistance to the spread of the excitations. But this contradicts the generally accepted view that exercise renders the paths of transmission less resistant to nervous excitations. It seems more reasonable to assume that the spread of the excitations is increasingly limited, as the inhibitory powers of the centres become developed.

In attempting the solution of the second difficulty, it is not enough to invoke the varying number of the tactile spots in various regions of the skin, because as Kiesow showed (see pp. 38-39) the extreme differences observed are never greater than 1 to 6·35, while the maximal diameters of the so-called tactile circles vary between 1 and 67 mm. To explain this fact on Bernstein's theory it is necessary to assume a subsidiary hypothesis, according to which the central spread of excitations arising from the regions in which the power of localisation is less well developed must be enormously in excess of the spread of excitations from regions in which the localising power is more highly developed. The improbability of this surmise is obvious.



FIG. 24.—Aristotle's experiment, in which there is an illusion of touching two separate objects with the index and middle fingers.

And, in reply to the third point, as the hypothesis of the transmission of local signs from the periphery to the centre cannot be accepted, we are forced to assume that the power of localising contacts at the periphery is purely and simply a consequence of the general law of the excentric projection of sensations. But this is merely the statement of a fact, not its scientific explanation.

In regard to this law, again, it is a matter of controversy whether the empirical or the nativistic theory should be applied to it. Aristotle's well-known experiment favours the former. When the index and middle fingers are crossed (Fig. 24) and an object is placed between the finger-tips, there is an illusory sensation of touching two distinct objects. The illusion is so strong that it does not vanish when controlled by sight, and it increases if the object is rolled between the fingers. Obviously this depends on the fact that the sensitive skin-surfaces are in an unusual position, owing to the crossing of the fingers. When the two fingers are in their normal position, we cannot touch an object simultaneously with the outer edges of the tips of the fore and middle fingers; two objects are required to produce the double sensation. Hence the illusion of two objects on crossing the fingers depends on the experience already impressed on our brain, which has become the general rule of our perceptions, *i.e.* of the un-

conscious judgments associated with our sensations. It is thus evident that the excentric projection and objectification of our sensations into the external world occur only according to the law of experience. Aristotle's illusion has recently been explained by Menderer and Ponzo in the above manner, but by a more subtle analysis.

They recognise the same cause for Aristotle's illusion, and use it to explain a number of other illusions. Among the latter is the converse observation discovered by Rivers, that on touching with two rods the edges of the fingers which face in opposite directions when they are crossed, there is an impression of only one rod between them. The same illusion is obtained on putting two objects under the tips of the crossed fingers, which are then confounded into one (Ponzo).

Other similar illusions have been observed and studied by Ponzo, in which, on displacing some part of the body, *e.g.* the lobe of the ear, from its normal position, the impressions are still referred to the region in space in which the displaced part is normally situated. Along with these we must group the so-called finger-exchange (Henri, Ponzo), in which when the fingers are crossed stimuli acting on one finger are referred to another.

The power of localisation at the cutaneous periphery is not confined exclusively to sensations of contact, but extends to all the cutaneous sensations. Ponzo has recently estimated errors in the localisation of tactile and pain sensations by pricking different parts of the body so as to stimulate single specific points. He found that the magnitude of the error varies with the region of the body. The maximal delicacy of localisation is found in the tip of the tongue, end of the forefinger, and middle part of the free border of the lower lip; the minimal in the lateral surfaces of the thorax. Sensations of cutaneous pain may be localised as exactly as tactile sensations (Ponzo); it is consequently a fallacy to suppose that pain sensations cannot be localised, or are so no less exactly than tactile sensations. Thermal sensations, too, are localised, but less accurately. A systematic study of this subject is wanting, but the experiments of Rauber (1869), of Goldscheider (1887), and the more recent work of Ponzo, show that cold spots are capable of more exact localisation than heat spots. The stimulation of two cold spots can be plainly appreciated at a distance of 0·8-3 mm., while in the same region that of two heat spots can be recognised separately only when 2-5 mm. apart.

Lastly, the power of distinguishing two punctiform contacts on the skin must not be confused with the power of localising them; similarly, two points viewed through a prism may be distinct from one another, and at the same time be localised in a position in space other than their real place. Thus, in observations made

by Schittenhelm and Spearman, in cases of lesions of the spinal cord, the power of localising sensations in the affected limbs was almost normal, but the patient was unable to discriminate the points of the compass applied to the thigh.

IX. Those sensations are termed *painful* which are characterised by an affective tone of physical or corporal discomfort, even when this is low in intensity. Certain olfactory and gustatory stimuli can produce disagreeable sensations even at their affective threshold: certain too vivid contrasts of colours, too harsh dissonances of musical tones, offend eye or ear. No one, however, speaking accurately, will apply the term painful to these sensations, in the sense that this term is applied to the discomfort produced by a wound or burn. *Pain* is a sensation *sui generis* which cannot be confused with the affective tone that sometimes accompanies the so-called specific sensations. Further, the sensation of pain is one of the simplest psychical states, and cannot be transformed into perception. We may feel pain without perceiving its cause and projecting it into the external world. When, on the contrary, we smell a bad odour, or taste a nauseating food, our disagreeable sensations are associated with the perceptions of something external to ourselves, which acts on our smell or taste. The same holds good for unpleasant auditory and visual sensations.

So, too, the specific cutaneous sensations (of contact, cold, or heat) are quite distinct from sensations of pain. It is true that on exciting any point of the skin by stimuli of excessive strength or duration we can easily provoke painful sensations, which with increased strength of stimulus may produce reflex cramps, mental disturbances, fainting, etc. But it would be a mistake to interpret this fact by assuming that there is a painful component inherent in sensations of pressure, warmth, or cold which increases disproportionately when the stimulus and the reaction to it become violent. In a moderate tactile or thermal sensation there is no trace of pain. A painful sensation aroused by too powerful compression of the skin never appears to any one on introspective examination as an excessive tactile sensation, although the stimulus is only a stronger application of the contact. The pain caused by a burn is not felt as a sensation of excessive heat. Both violent compression and excessive heat when applied to the skin produce intense pain that dominates the specific sensations of pressure or heat, and suppresses them altogether.

This brings us to the question whether the nerves and the specific end-organs for pressure, heat, and cold are also capable of giving rise to sensations of pain when excited by excessive stimulation (as assumed by Hagen, Lotze, Wundt, Richet, and others), or whether the skin contains specific nerve-endings and the central nervous system distinct centres for pain sensations,

considered as a special modality of cutaneous sensation (as held by Brown-Séquard, Funke, Münsterberg). We have already seen that the more recent work of v. Frey and Kiesow is decidedly in favour of this view, and must now investigate the arguments on which it is founded.

Funke (1880) was the first to call the attention of physiologists to the interesting clinical observation that a *dissociated paralysis* of pain sensibility is possible while other specific modalities of cutaneous sensation remain normal. Special forms of dissociation of the different forms of cutaneous sensibility have been described since Weber's time in a number of cases of spinal disease (spinal compressions, traumatic spinal lesions, syringomyelia, tabes dorsalis, etc.) Analgesia with integrity of sensibility to contact, cold, and heat is not uncommon; it not merely involves the skin, but may also extend to the deeper tissues, the muscles, the bones, and the mucous membrane. The case cited by Weber of the Swiss physician Viessaux (1818) deserves mention. He was attacked by spinal disease, and noticed with surprise that the fingers of his right hand could be wounded or crushed without producing any pain, although he was able to detect all the clinical characters of the pulse with them. In this case of dissociation of cutaneous sensations the post-mortem examination showed a lesion confined to the dorsal horn of the spinal grey matter, which agrees with the view of Schiff and Budge.

How is such isolated analgesia to be explained, if we assume that the peripheral and central organs for pain sensibility are the same that subserve tactile and thermal sensations? As Funke correctly remarks, it would be paradoxical to assume that those peripheral and central organs which subserve tactile, thermal, and pain sensibility could become inexcitable to the strong stimuli that are necessary to induce pain, and at the same time preserve their excitability to the slight stimuli that suffice to produce tactile and thermal sensations. To account for the phenomenon of isolated analgesia it is necessary to admit either that from the spinal cord up to the brain the pain paths are separated from the tactile or thermal paths, as assumed by Schiff, or that the former are already distinct from the latter at the periphery, and that the skin contains specific nerve-endings for pain, other than those for tactile and thermal sensibility. Funke leaves the question open.

In his investigations with point stimulation, Blix observed that every here and there the point of a needle could be pushed deep into the skin without producing the least sensation of pain, while in other parts a slight prick with the needle did cause pain. But his investigations into pain sensibility did not furnish facts to justify the assumption of pain sense-organs anatomically

distinct from those of the other modalities of cutaneous sensation.

Goldscheider succeeded in proving that the cutaneous spots for heat and cold are normally analgesic; that pressure spots, on the contrary, when excited with strong stimuli give rise to intense pain; and that the area surrounding the pressure spots (and provided, in his opinion, with nerves of common sensibility) reacts to tactile and pain stimuli, but far more feebly than the pressure points.

Von Frey obtained different results from his wider and more accurate researches. He showed that with suitable mechanical stimuli it is possible to demonstrate the existence of well-circumscribed spots, which do not usually coincide with the tactile spots, in which sensibility to pain is maximal. To obtain pain sensations unaccompanied with sensations of pressure or contact, it is necessary to use sharp points, to moisten the epidermis previously, and to excite the skin where the touch spots are far apart. Even with chemical stimuli, and under certain conditions with electrical stimuli, it is possible to produce isolated sensations of pain.

Pain spots are distinguished from tactile spots by a longer latent period, and by being four times as numerous (on an average more than 100 to 1 sq. cm.).

There is also a marked difference in the minimal value for mechanical stimulation between tactile points and pain spots, according to the area of the excited surfaces. On stimulating surfaces of 3-12 sq. mm. the sensibility of the nerve-endings to pressure is a thousand times greater than that to pain (v. Frey). But as the excited surface diminishes, a given mechanical stimulus becomes gradually more effective for the pain spots, till with a minimal surface the threshold for pain may be lower than that for pressure.

It was formerly believed that there could not be pain unless the skin were excited with stimuli strong enough to act directly on the subjacent nerves (Weber). But more careful investigation has proved that it is possible to excite pain with such weak mechanical (v. Frey) and thermal (Thunberg) stimuli that all direct excitation of the nerve-fibres must be excluded. It is further to be noted that when the skin is excited by effective instantaneous stimuli (mechanical or thermal) the sensation of pain has a very long latent period (0·9 sec.). While on the one hand this excludes the hypothesis of any direct action on the nerves, which never have this enormous latent period of excitation, it shows on the other hand that the stimulus acts on nerve-endings which are capable of transforming weak stimuli into neural excitation by some physico-chemical process (v. Frey).

The topography of the pain sensibility of the skin (*cutaneous algesimetry*) has been the subject of much research, mainly from a

clinical point of view. But owing to the imperfect methods employed, the results are very scanty and do not seem worth mention. Taken as a whole they show that the dissimilar sensibility to pain of different regions of the skin depends largely upon the varying depth of the horny layer. Not improbably it also depends on the varying number of the pain spots in different regions, but methodical investigation of this difficult and delicate subject is still wanting.

We saw above that the cornea is rich in pain spots and contains no true touch spots; the conjunctiva of the eye and the glands are rich in cold and also in pain spots; the mucous membrane of the cheeks, the posterior part of the buccal cavity, the posterior part of the tongue, have little sensitiveness to pain. According to Kiesow's observations, in some parts of the mucous membrane of the cheeks (*e.g.* those corresponding to the second lower molar) pain spots are entirely absent: pain is not produced here by the strongest mechanical and electrical stimuli.

Comparison of the results obtained on exciting the pain spots and touch spots respectively shows the following differences:—

(*a*) The threshold of sensibility to punctiform mechanical stimuli is, generally speaking, higher for pain spots than for touch spots; but the relation between the two thresholds varies in the different regions and may be reversed (v. Frey).

(*b*) The threshold for electrical stimuli (faradic currents applied by the unipolar method) is higher for touch than for pain spots.

(*c*) Faradisation of the pain spots at a frequency not exceeding 20 shocks per second arouses a continuous sensation, while faradisation of the touch spots up to a frequency of 130 per second produces discontinuous sensations of vibration.

(*d*) The latent time for pain is always much longer than for contact. The after-effect also is incomparably longer (Richet).

(*e*) The sensation aroused by the stimulation of a tactile spot is projected to the surface of the skin, and may be confined to one spot; the sensation of pain aroused on stimulating a pain spot seems to spread superficially as well as deeply, and has no precise local sign. But, according to Ponzo's latest work, pain sensations too are projected to the cutaneous surface and localised there.

(*f*) Cooling of the skin produces hyperaesthesia, followed by loss of sensibility. The paralysis of the pain spots invariably precedes that of the touch spots. Cocaine applied to the tongue abolishes first tactile and then pain sensibility.

When we reflect on the teleological importance of sensibility to pain, it is readily seen to be one of the most effective weapons of defence of the organism; but it appears to be unequally developed at different degrees of the animal scale. We have no

proof that it exists in the lower animals. By a minute analysis of the motor reactions of *Lumbricus*, Normann has proved that they cannot have the significance of expressions of pain, because the same reactions are seen in the segments with and without nerve ganglia. Loeb found that if a *Planaria* was divided in half, the anterior part continued to move quietly as though it had felt no pain. In *Gammarus* the stomach can be cut away during copulation without interrupting it. Bethe noticed that the abdomen can be cut off a honey-sucking bee without disturbing its occupation. The frog reacts violently to electrical stimulation of the sciatic nerve, but whether it feels much pain is doubtful, as the same reactions take place after decerebration. Herbivora are less sensitive to pain than carnivora. Veterinary surgeons know that horses continue to eat while undergoing an operation, and the rabbit eats directly after serious operations. These and other observations show that the development of sensibility to pain is parallel to the development of the intelligence. In human races sensibility to pain is more developed in proportion as they are more civilised: in imbeciles, idiots, and dements it is very low.

Pain, then, is a function of the intelligence, a psychical element superposed upon the subconscious protective reflexes. A painful sensation produced by a mechanical or thermal agent at the cutaneous periphery may from the teleological point of view be compared with the nauseating taste of a poison. Weber observed that the temperature which began to produce pain (48° C.) when applied to the skin was the same at which the nerve substance begins to alter. The teleological relation between the painful stimulation of certain afferent paths and certain instinctive reactions witnesses to the protective significance of pain.

Nevertheless, it cannot be affirmed that pain is an infallible indication of menace to life. There may be severe pain, as in neuralgia, with no manifest lesion of the tissues: at other times there may be no pain although the tissues are fatally affected, as occurs with an invasion of pathogenic bacteria. This shows that in the world of living beings co-ordination of function to a given end takes place within definite limits, and that the sense-organs, like all the other organs, are adapted to function teleologically during normal relations with the environment, and not in exceptional circumstances.

Whether the sensations of *tickling* and *itching* are to be considered as specific sensations in the same category as sensations of pressure and of pain, or merely as modifications of the latter, is still a matter of controversy. We must first examine the conditions which give rise to them. To arouse tickling in the cutaneous regions provided with hairs, it is only necessary to touch these parts lightly, *e.g.* by a feather. Even in the parts that have no hair—the red of the lips, the nostrils, eyelids, and

forehead—the slightest touch will arouse tickling and a desire to scratch to remove the annoyance. In these parts it is not necessary to excite with light and delicate stimuli: coarse mechanical stimulation will arouse such a tickling that it causes violent reflex movements spreading to almost all the muscles, and uncontrollable by the will.

The sensation of itching which accompanies different cutaneous diseases is normally produced by the sting of an insect, and may readily be aroused by the prick of a fine needle. But Jessner holds, on the contrary, that itching is a paraesthesia, *i.e.* a morbid variety of cutaneous sensibility that is absent in normal individuals.

There is no very marked difference between the sensations of tickling and itching: there are intermediate sensations, which may be regarded as mixed sensations, due to the simultaneous excitation of several sense-organs.

According to Weber, tickling depends on a diffusion of the excitation, and on the persistence and increase of the sensation after the stimulation has ceased. Funke, too, regards tickling as a secondary effect of sensations of contact, which only arises on applying weak stimuli. Goldscheider, who, as we saw, ascribed pain sensibility to the pressure end-organ, refers tickling also to a special mode of excitation of the same organ. Von Frey and Kiesow, on the contrary, hold the organs for pressure and pain to be distinct, and refer the sensation of tickling to the first, of itching to the second. With Quincke they regard tickling and itching not as primary, but as secondary sensations, caused by reflexes acting from the nerves of touch and pain upon the vaso-motor nerves. But on what does the peculiar feeling of these sensations depend? Why do they arise with weak stimulation and disappear when the stimulus is strengthened? These questions are unsolved.

Alrutz has disputed the theory of v. Frey and Kiesow. He considers that tickling and itching are two varieties of a single modality of sensation, depending on special nerves other than those of pressure and pain. He states that the sensation of tickling is produced by excitation of cutaneous spots other than the touch and pain spots. He quotes a case of lead-poisoning described by Bean, in which there was analgesia without disturbance of pressure sensibility, but with insensibility to tickling. In two other cases of circumscribed or diffuse analgesia he observed the same state, that is, persistence of tactile sensibility in parts insensitive to tickling. He further cites a case of hyperalgesia communicated by Goldscheider in which there was hyperaesthesia for sensations of tickling and itching. These must accordingly run parallel with the pain sense and not with tactile sensibility.

It remains for further researches to decide which of these opposing theories is correct.

EDITORIAL NOTE

This chapter would not be complete for English readers at least without a reference to the investigations of Head and Rivers on the mechanism of peripheral sensibility. Their conclusions were drawn mainly from a study of the sensory changes produced by section of a small cutaneous nerve in Head's arm and the observation of the sensory phenomena that occurred during its regeneration, but they were supported by numerous clinical examinations made in conjunction with Sherren.

In addition to those fibres concerned with cutaneous sensibility, they described a system that subserves *deep sensibility* (see Chapter II.) the end-organs of which respond to pressure either by sensations of contact or of pain if the pressure is excessive, and to the movements of joints, tendons, and muscles. The sensations of pressure evoked can be accurately localised, and the direction of the movement appreciated correctly, even though the overlying skin is totally insensitive, but two compass points applied simultaneously over the part cannot be discriminated by this system alone. The nerves of this deep sensibility run mainly with the muscular nerves and are not destroyed if all the cutaneous fibres are cut. Head and Thompson, however, suggest that fibres belonging to the deep system also reach the skin.

Cutaneous sensibility was divided into two separate systems; the one called "*protopathic*" is capable of reacting to all painful cutaneous stimuli of every nature, and to the more extreme degrees of heat and cold, that is, to thermal stimuli above 40° C. and below 24° C., but the sensations produced are diffuse, unnaturally intense, and unaccompanied by a definite recognition of the locality of the spot stimulated.

Through the second system, styled "*epicritic*," light contact and the intermediate degrees of heat and cold are appreciated, and on it, in addition, depends cutaneous localisation, the discrimination of the compass points, and the appreciation of size.

The protopathic system is essentially one of punctate sensibility, as sensations of pain, heat, and cold can be excited only from the corresponding spots; the sensation of warmth depends probably on nerve-endings that lie between the sparsely scattered heat spots, and the appreciation of coolness, as contrasted with cold, may be due to end-organs other than those of the cold spots.

It is suggested that these three peripheral systems were developed at different phylogenetic periods. The two cutaneous systems, the so-called "epicritic" and the "protopathic," can be, according to Head, studied separately on an area of skin after section of a sensory nerve, as the loss of the protopathic elements is usually less extensive than the epicritic, and during regeneration and recovery of function, since the "protopathic" sensibilities reappear first. On the glans penis, too, there is only "protopathic" sensation.

These ingenious and elaborate observations have not been, however, verified or supported by authoritative independent investigations, and the researches of Trotter and Davies, especially, have thrown much doubt on them and on the accuracy of the conclusions drawn from them. These workers investigated the effects of the section of seven cutaneous nerves in themselves; they found that this operation produces a central area of profound sensory loss, an intermediate zone of moderate extent surrounding this of partial loss, and a larger zone in which qualitative changes only can be detected. When regeneration sets in, the return of all sensory functions begins about the same time, but is irregular. They failed to discover that identity in the states of sensation in the intermediate zone of partial loss and in the central area during the progress of recovery, which is an essential

point in Head's theory, and they could not confirm the simultaneous return of sensibility to touch and to moderate degrees of temperature in the same areas, on which Head's hypothesis largely depends.

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CHAPTER II

SENSIBILITY OF THE INTERNAL ORGANS

CONTENTS.—1. Classification of internal sensations. 2. Common sensation of the body or *coenaesthesia*. 3. Pain in the internal organs and tissues. 4. Alimentary needs (hunger and thirst). 5. Sexual desire. 6. The muscular sense: sensibility of muscles, tendons, and joints. 7. Innervation sense in the centres of voluntary movement. 8. Active tactile perceptions and their components. 9. The subconscious sense of muscular tone and its variations in reference to the functions of the labyrinth. Bibliography.

ALL internal organs and tissues provided with afferent nerves have a greater or less degree of sensibility. The sensations aroused from the peripheral terminations of these nerves are almost always independent of external stimuli, and depend as a rule upon the somatic conditions inherent in the organism. They are accordingly grouped together under the name of Internal or Bodily Sensations.

While the specific sensations aroused by the action of the outer world are the basis from which our intellect is developed and perfected, the internal sensations do not normally give any clear indications of our internal world. Nevertheless they are of great importance from the psychological and philosophical point of view, as was well brought out by Cabanis at the beginning of the last century in his famous book *Rapports du physique et du moral de l'homme*. He showed that, even when they do not pass the threshold of consciousness, the internal sensations may send impressions to the brain which alter our psychical personality. On the other hand we know that they exercise reflexly, along the efferent nerves, a controlling influence upon all the functions of the vegetative and animal life.

I. The physiological study of the internal sensations of the organs has progressed very little because their indefinite character usually makes a strict application of experimental methods impossible. Physiologists have been content to hand over the study of this category of phenomena to clinicians, who have frequent opportunities of investigating them in their patients, in whom they are often exaggerated and become more conspicuous.

or are, on the other hand, suppressed so that the effects of deficiency can be studied. Few physiologists have attempted to classify them according to rational criteria. Magendie seems to have been the first who divided the internal sensations into four groups, on a physiological basis:—

(*a*) The first come into play when it is desirable that the organs should function. This group comprises the wants, desires, and instinctive appetites that originate from a too protracted abstinence. Such are hunger, thirst, desire to micturate or to defaecate, sexual desire, etc.

(*b*) The second appear during the activity of the organs. They are often obscure or quite subconscious sensations; but may be urgent, as the sensations felt during the excretion of urine or faeces, and especially during ejaculation, which is the culminating point of sexual activity. Highly important among the sensations of this group, and one of the best studied, is that of *tension*, *constriction*, and *effort* felt during muscular activity, by which we judge of the range, speed, direction, and energy of our movements.

(*c*) The third group includes the feelings that arise after protracted or energetic action of the organs. Such is the sense of fatigue that succeeds after too prolonged or excessive activity of the muscles, drowsiness after long waking, the feeling of exhaustion and languor after sexual indulgence, of satiety after a full meal, etc.

(*d*) The fourth group includes the innumerable internal sensations associated with illness, which range from a vague general sense of discomfort to more or less acute and diffuse pain. In this group we may include the shivering which ushers in attacks of fever, the heaviness and burning in the head which is more or less characteristic of febrile processes, the vertigo often present in attacks of nervous illness, the nausea that precedes vomiting, the so-called "visceral hallucinations," etc.

However ingenious this classification may be it is incomplete. It omits two other groups of bodily feelings, which are no less important in their effects although vague and indefinite in character, so that it is doubtful whether they normally cross the threshold of consciousness. These are:—

(*e*) The common sensation of well-being or coenaesthesia concomitant with the state of perfect health, which is expressed in adolescence by a more or less accentuated exuberance of movement.

(*f*) The obscure feeling by which we become aware of the position of our body and its individual parts (head, trunk, limbs); and the equally obscure sense of equilibration and orientation of the body in respect of the external world, in so far as these can be independent of the active state of the muscles and the specific external senses.

Many of the bodily feelings thus classified escape physiological analysis owing to their vague and obscure character. Of others we know little, and that little claims no special mention here, either because it falls within the domain of common observation, or because it comes into the special department of neuropathology and psychiatry. We must here confine ourselves to the more important physiological points that have been cleared up.

H. Henle gave the name of "common sensation" (*Gemeingefühl* or *coenaesthesia*) to "the sum, the confused chaos of the sensations which are incessantly transmitted to the brain from all the parts of the body." Normally we have no clear and distinct consciousness of the functions of the internal organs and tissues, but we undoubtedly have a dull and obscure knowledge of them, similar to that of the sensations that provoke and accompany the respiratory movements. We have in short an incessant awareness of our body, which Condillac termed the "fundamental sense of existence," and which is the link between psychical and physiological life. In the state of equilibrium that constitutes perfect health, this feeling is continuous, uniform, and always equal, so that it remains at the threshold of consciousness, and is prevented from becoming a distinct sensation with special characters and specific localisation. But when it reaches a certain intensity it is perceived as a vague sense of general well-being or the reverse. The former, known to clinicians as *euphoria*, is the expression of an exaltation of the physiological functions of the organs, the latter of their disorder, transmitted to consciousness by the cerebro-spinal sensory nerves, or by the afferent nerves of the sympathetic system.

"It is probable," Foster writes, "that sensory impulses, not of the character of pain, are continually, or from time to time, passing upwards from the abdominal viscera to the central nervous system. These do not affect our consciousness in such a distinct manner as to enable us to examine them psychologically in the same way that we are able to examine special sensations such as those of sight, or even sensations of pain; they are even less well-defined than those of the muscular sense; nevertheless they do enter, though obscurely, into our consciousness, so that we become aware of any great change in them."

A striking proof of the real existence of common sensation is seen in the fact that in certain morbid cases it may be wholly or partially suppressed. In some forms of mental disturbance, in certain cases of anaesthesia or partial paralysis, the patients have no sensation in one part of the body (*e.g.* in one limb, the stomach, the brain, etc.), or from some cerebral disease sensation in one part is abnormal—*e.g.* the patient fancies he has a glass or wooden arm. More rarely there is a total abolition of coenaesthesia. It is said that the obstetrician Baudelocque in the last days of his life lost

consciousness of his own body. Probably the same phenomenon takes place in insane subjects who speak of themselves in the third person. All the alterations and perversions of organic sensibility, of which Ribot gave a brilliant analysis in his *Maladies de la personnalité*, come into this group of phenomena, since coenaesthesia is the physical basis of individual personality.

Can the sensibility of the internal organs be so extended and intensified that the work of the organs of vegetative life, which is normally carried on unconsciously, may reach consciousness? Is the threshold of consciousness at a fixed and constant level, or does it oscillate, and can it under certain extraordinary or abnormal conditions drop so much that its range is correspondingly increased and widened? This question is as important as it is delicate. Reliable authors who have concerned themselves with *hypnosis* and other similar states (Beaunis, Liebeault, and others) affirm that many persons have in the hypnotic state a more or less clear sense of the organic changes and of normal or morbid states that occur within the organs of vegetative life. It is well authenticated, according to Beaunis, that during hypnotic sleep and even in the somnambulist waking state, all the functions of vegetative life can be modified by suggestion—the pulse rate can be altered, redness and persistent congestion can be produced in certain regions of the skin, cutaneous haemorrhage can be induced, the menstrual flow can be diminished, increased, or regulated, the different secretions (tears, sweat, milk, urine, intestinal juices) can be excited or arrested, uterine contractions similar to those of parturition can be produced, the temperature of the skin raised, and lastly, blisters formed in the skin. These surprising phenomena show that the brain is able under certain conditions to transmit a centrifugal effect even to the organs of vegetative life, and to affect their activities as it does the muscles of animal life, and implies the existence of a centripetal current from these organs to the brain, by which it may receive a more or less distinct sensation of the processes going on in the organs. In order, says Liebeault, to explain the suggestive action of thought on the tissues as a whole during somnambulism, it is necessary to admit that the brain which transmits orders to the glands, blood-vessels, etc., is aware of the sensations that come from them.

Apart from his spiritualist convictions, the posthumous work of F. W. Myers on "Human Personality" contains a fund of incontrovertible facts which have not yet been analysed by the physiologist. Some of these observations show that the threshold of consciousness is not fixed and invariable, but may alter considerably, spontaneously or artificially, in different states of the nervous system occurring in individuals who are specially predisposed or trained by special education.

III. From the practical point of view the commonest and

most important modality of exaltation and perversion of the sensibility of the internal organs and tissues is certainly represented by *pain*, in its various forms and varieties.

In the last chapter we examined pain as one of the distinct modalities of cutaneous sensibility, having nerves and nerve-endings different from those of the other sense-organs of the skin. But unlike the senses of pressure and of cold and heat, the sense of pain is not specific, but belongs to the group of internal senses that give rise to sensations that are incapable of transformation into perceptions. It further differs from the other cutaneous sensibilities in certain important characters: it is not excited by special *adequate stimuli*, but can be aroused by any kind of stimulation (mechanical, thermal, electrical, chemical) that is capable of acting on the nerve-fibres along their course; it has incomparably longer periods of latent excitation and after-excitation; the pain impulses have a greater capacity of summation so that the sensation is rendered continuous; and lastly, they have a greater tendency to spread in every direction and have no precise local signs, excepting the cutaneous pain spots which—according to Ponzo's recent work—can be localised as exactly as the touch spots.

The sensitiveness of the skin to pain is only a more evolved and perfected form of the common sensibility proper to all internal tissues that possess afferent nerves. This theory is by no means new. The earliest physiologists distinguished *pain*, either cutaneous or of the internal tissues and organs, from the specific sensations, and referred it to the group of crude sensations—hunger, thirst, nausea, fatigue, etc. But, since on the ground of v. Frey's work, the existence of special nerves and nerve-endings for pain, constituting one of the cutaneous senses, is now admitted, it must be asked whether these are capable only of reacting by pain-sensations to every kind of stimulus, or whether (like the afferent nerves of the internal organs and tissues) they can also react by obscure and non-painful sensations, *i.e.* can they transmit subconscious sensations to the centres on normal weak stimulation, and sensations of greater or less pain, which is more or less conscious, on abnormal excessive stimulation? All the evidence is in favour of this last supposition.

We have seen that pain is not a primordial form of sensibility, but that, in the animal series, it develops along with the development of intelligence, and is psychically superposed on the protective subconscious reflexes, the better to protect the individual from the injurious action of the outer world. As Foster pointed out, "It may happen to a man to suffer pain in a particular region or tissue of the body once only in the course of his life-time, or possibly not even once; nay, we may suppose that in this or that region or tissue pain is felt once only in one individual among a large number of persons." In such a case, if there really

were special organs destined exclusively for sensations of pain, we should be "driven to conclude that such . . . a mechanism of pain has been preserved intact but unused through whole generations in order that it may once in a while come into use, which is in the highest degree improbable. This difficulty disappears if we suppose that the constantly smouldering embers of common sensibility may be at any moment fanned into the flame of pain."

So that, if we assume with v. Frey that there are numerous pain spots in the skin with corresponding nerves and end-organs, this does not mean that there is a specific apparatus exclusively intended to serve pain sensibility; it is the same that subserves the common sensibility of the internal organs and tissues, and normally transmits subconscious excitations only. Granting this to be reasonable, it does not therefore exempt us from examining whether the afferent nerves of the internal organs have normally, like those of the external tegument, the capacity for arousing pain, when artificially stimulated with excessively strong stimuli. This question is very important from a practical point of view.

The physiologists of the seventeenth and eighteenth centuries were much occupied in testing the sensibility of the internal parts to pain in animals, and many important surgical observations were also made on man previous to the introduction of ether and chloroform narcosis. The introduction in recent times of the method of local anaesthesia, specially by cocaine for major operations, has opened a new era in the study of this subject, making it possible to test the sensibility of the different tissues. But the results are at present contradictory or uncertain.

The general results obtained from the whole of these observations, new and old, may be summed up as follows:

(*a*) Only the tissues provided with nerves are sensitive to pain stimuli: the epidermis, the horny tissues in general, the cartilages and fibro-cartilages are totally insensitive, because they have no nerves.

(*b*) The organs, tissues, and internal membranes innervated by the sensory roots of the nerves of the cerebro-spinal axis are more or less sensitive to painful stimulation.

(*c*) The organs and internal tissues innervated exclusively by the nerve-fibres of the sympathetic system are little sensitive to pain stimuli under normal anatomical and functional conditions, but in a state of inflammation they may acquire an exquisite sensibility to pain.

There are no exceptions nor comments for the first proposition; the second and third, on the contrary, must be examined. The connective tissues, ligaments, tendons, and aponeuroses have, under normal conditions, an indefinite sensibility to pain. The periosteum is very painful, as shown on scraping the bones in certain surgical operations; but bone itself, particularly the

compact substance, is insensitive, as proved in amputations without chloroform. The pain sensibility of bone-marrow under physiological conditions is doubtful.

The muscles in the normal state are but little sensitive to pain. During amputations without anaesthetics they give no pain. Strong compression gives rise to a specific dull pain; intense faradisation is very painful. This sensitiveness to pain is not due to excitation of the cutaneous nerves, because Duchenne observed it with direct electrical stimulation of the pectoralis major muscle exposed during excision of the breast. The feeling of muscular fatigue presents every gradation from a simple sense of heaviness to acute pain, which may last 24-48 hours, and is accentuated on the slightest pressure. But in this case the state of the muscle is evidently altered, owing probably to the accumulation of fatigue products, which act as an irritant poison. Similar abnormal conditions underlie the muscular and articular pains of a rheumatic and gouty character. On the other hand, the sharp pain that accompanies the cramp caused by violent and involuntary contracture of the muscles is transitory. It has been attributed to the compression of the cutaneous sensory nerves that traverse the muscles, but this is a fallacy, because in that case, in accordance with the law of peripheral projection, the pain would be perceived in the skin and not in the contractured muscle.

Serous membranes in general, as the peritoneum, pleura, cerebral and spinal dura mater, and the synovium, are believed to be sensitive to pain even under normal conditions, and when inflamed become much more so.

The pain sensibility of the mucous membrane of the digestive tract is generally very acute near its junction with the skin (oral and pharyngeal cavities), but it diminishes in the oesophagus. The painful sensation of choking produced when an alimentary bolus that is too large or too hard sticks near the cardiac aperture of the stomach is not due solely to the sensibility of the mucous membrane, but rather to the cramp that compresses the nerve fibres that surround the canal. The pain sensibility of the stomach is moderately acute, that of the intestine low, but it increases again in the rectum and at the anal orifice. Puncture, section, cauterisation (as shown by experiments on rabbits and dogs, and surgical operations in man), do not produce true sensations of pain in any part of the intestinal canal under normal conditions. But in a pathological state, the intestine may become the seat of severe pains, such as those of colic.

The mucous membrane of the respiratory apparatus is sensitive to pain in the nasal and laryngeal tracts, but insensitive throughout the bronchial ramifications.

The mucous membrane of the ureto-genital system is very

sensitive along the urethral canal, particularly in the prostatic or membranous part; that of the bladder, on the contrary, has little sensibility. Even large calculi may remain unperceived for some time until inflammation sets in. The vulva is sensitive, but the vagina, cervix of the uterus, and the uterus itself are only moderately sensitive. As long as they are normal they can be cut or cauterised without producing pain. Pain in these parts undoubtedly depends on compression or traction of the sensory nerves that lie in the depths of the tissue, or in the uterine appendages and the vaginal canal.

The excretory ducts of the glands are usually very sensitive to distension. The intense pain of hepatic and nephritic colic is well known.

The heart, arteries, and veins are insensitive to pain in the normal state. The same may be said of the hepatic parenchyma, spleen, pancreas, kidneys, and lymphatic glands. The genital glands, the testicles, the ovaries and their appendages are, on the contrary, highly sensitive. Compression of these parts causes acute pain, and may even induce syncope.

From all these facts it is clear that the internal tissues and organs have as a rule a lower sensibility to pain than the surface of the body; and that the deep organs innervated by the sympathetic normally feel little pain, but they have a very high latent pain sensibility which may become apparent under abnormal conditions, particularly in inflammation.

Lennander (1902 4), on the basis of a new series of clinical observations, opposed this hypothesis, and maintained that the difference of sensibility shown by the internal tissues, according as they are in normal or pathological states, is to a large extent apparent only. According to his observations, the pains that can be produced in the abdominal cavity must be referred to the parts innervated by the lumbar and sacral nerves, particularly those to the parietal peritoneum. This is sensitive under both normal and abnormal conditions, especially to mechanical stimuli (traction, dilatation); while the whole of the intraperitoneal viscera and the visceral peritoneum which covers them are, on the contrary, incapable of initiating pain either in the normal or the pathological state. When these viscera are diseased, the pains do not indicate exaggeration of their normal obscure sensibility; they remain insensitive, but transmit the irritation to the sensitive parietal peritoneum, either by an exaggerated peristalsis, or by *meteorism* or abnormal distension of the intestinal canal, by the traction due to inflammatory adhesions, or lastly by the production of toxines or irritative chemical products. The hyperalgesia of the parietal peritoneum caused by these products fully explains the fact that in acute abdominal diseases the weakest stimuli may provoke very intense pain.

According to Lennander, the same holds for the thoracic and cranial cavities. The lungs and visceral pleura are insensitive, and the pains felt in the chest in certain illnesses are caused by the transmission of excitations to the parietal pleura, which is sensitive under normal conditions also.

The brain is insensitive, and the pains in the head so frequently felt are due to transmission of excitation to the dura mater.

Generally speaking, Lennander holds it probable that all the organs innervated by the sympathetic alone, and by the branches of the vagus after the separation of the recurrent nerve, are insensitive to pain, not merely in the healthy but also in the inflammatory state.

This statement does not seem to be justifiable, at any rate not in such a general form. How can we deny the sensitiveness to pain of the bile duct, the ureter, and the intestinal tract in cases of gall stones, of hernia, and of other forms of obstruction of the digestive canal? On the other hand, the work which Ducceschi carried out in our laboratory "*On the nerves of the stomach*" (1905) shows clearly that mechanical, thermal, and electrical stimuli applied to the outer surface of the stomach of normal dogs and cats cause obviously painful reactions (general agitation, disturbed respiration, cries, characteristic movements of the tail, similar to those made by the cat when it is hurt by stimulation of the cutaneous sensory nerves). The reactions are seen even after section of both vagi, or both splanchnics; they only cease when both have been cut. "It is interesting," writes Ducceschi, "to note that the stomach in certain cases seems to become more sensitive in proportion to the time that has elapsed since its exposure. Simultaneously with the increase of sensibility in the stomach, cutaneous sensibility declines. At the end of the experiment, after about two hours, a slight tap on the wall of the stomach causes strong general reactions, while pinching the ear, paw, or the skin of the abdomen does not cause even the slightest reaction. There is evidently shock of the peripheral sensory apparatus, accompanied by gastric hyperaesthesia."

From Lennander's latest communications it appears probable that the mucous membrane not only of the rectum, vagina, and uterus, but also of the ovary, oviduct, and ligamenta lata are insensitive to pain. All these parts can, he says, be operated on without pain to the patient, provided there is no traction of the connective tissue by which they are united to the walls of the pelvis and the parietal peritoneum. Probably the testicles and epididymis too contain no nerves of pain, though the parietal fold of the tunica vaginalis is highly sensitive. We must reserve our opinion on these theories also.

In opposition to and parallel with the clinical observations of Lennander, the clinical theory of *referred pain* has recently

assumed great physiological importance. Lange was the first who considered the pains and cutaneous hyperaesthesia that accompany certain diseases of the internal organs that are little sensitive, or insensitive, to be reflex. Since the work of Ross (1888), of Mackenzie (1892), and specially the more detailed

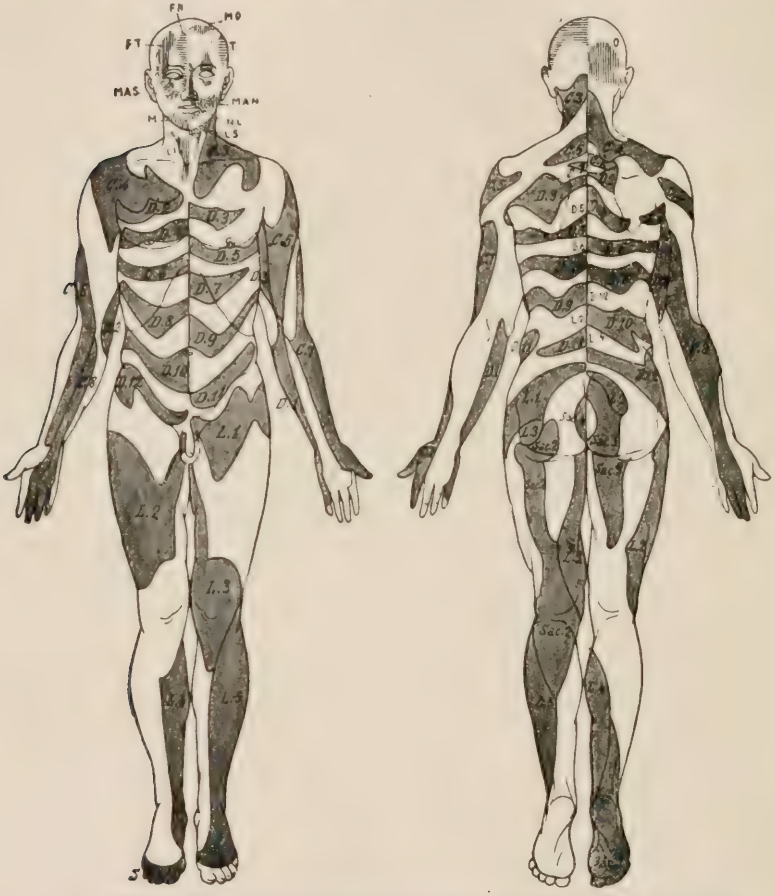


FIG. 25.—Diagram of zones and areas of hyperalgesia, after the clinical researches of Head. Explanation on p. 68.

observations of Head (1898), the theory of referred pain has acquired great interest, and in view of the modern segmental theory is of marked theoretical importance.

According to Head, certain morbid conditions of the internal organs are capable of provoking painful sensations, but these are almost always falsely located, *i.e.* in a part other than that affected. In the diseased organ, too, abnormal sensations

are often felt, but these are not so much true pain as an obscure feeling of heaviness or strain, while true, sharp, stabbing pain is projected to the surface of the body. According to Head, this false localisation is an effect of the low sensibility to pain of the internal organs and tissues, and of the connection between these



FIG. 26.—Diagram of zones and areas of hyperalgesia, after the clinical researches of Head. Explanation on p. 68.

and the nerve-centres of the much more sensitive external tissues. Head's law of the localisation of pain runs as follows:

"When a painful stimulus is applied to a part of low sensibility in close central connection with a part of much greater sensibility, the pain produced is felt in the part of higher sensibility rather than in the part of lower sensibility to which the stimulus was actually applied."[1]

[1] *Brain*, 1893, vol. xvi. p. 127.

The internal organs are, generally speaking, less sensitive than the skin; their afferent nerves are, according to Head, in close relation with the centres of the cutaneous sensory nerves of the same spinal segment.

The same theory applies, according to Head, to the cutaneous hyperalgesias observed in visceral affections. When abnormal excitations from a diseased internal organ reach the cord by way of the afferent nerves the excitability of the spinal segment becomes exaggerated, so that when another cutaneous excitation of low intensity reaches the same segment it provokes pain, whereas under normal conditions it arouses merely a sensation of contact.

These views were strengthened by Head's mapping out of the hyperalgesic zones that are observed in different affections of the viscera. Each diseased organ produces hyperalgesic zones which are characteristic in form and localisation. According to Head the zones of *herpes zoster* coincide with those present in hyperalgesia.

Head's hyperalgesic zone corresponds not with the areas to which the cutaneous nerves are peripherally distributed, but with those supplied by the dorsal roots. As shown in Figs. 25 and 26, these do not overlap, while the cutaneous metameres or dermatomes of the dorsal roots, on the contrary, according to Sherrington, do overlap to a large extent. But Sherrington's later work showed the overlapping to be different for different qualities of sensation; it is much more extensive for tactile sensation, much narrower for pain sensation. We saw (Vol. III. p. 306) that the work of Winkler and van Rynberk on the central area of dermatomes has thrown new light on this subject. And it is probable that Head's hyperalgesic zones represent segmental zones of Sherrington's pain areas, or of the central areas of the dermatomes of Winkler and van Rynberk.

Head's clinical investigations have such great practical importance that it is desirable to reproduce the following diagram and table, which sum up his results.

Figs. 25 and 26 show the segmental cutaneous areas of the trunk, extremities, and head. The form and extent of these were arrived at:

(*a*) by mapping out the areas in a number of cases of cutaneous hyperaesthesia with coincident visceral affections;

(*b*) from the topography of the eruptions in 52 cases of *herpes zoster*;

(*c*) by mapping out the analgesic areas in organic diseases of the spinal cord and roots.

The 8 cervical segments are indicated by C1, C2...C8; the 12 dorsal or thoracic segments by D1, D2...D12; the 5 lumbar segments by L1, L2...L5; and the 4 sacral segments by Sac. 1, Sac. 2...Sac. 4.

The areas of the head are indicated as follows: N = nasal or rostral area; FN = fronto-nasal area; MO = medio-orbital area; FT = fronto-temporal area; T = temporal area; V = vertical area; P = parietal area; O = occipital area; NL = naso-labial area; Max. = maxillary area; Man. = mandibular area;

M = mental area; LS = superior laryngeal area; LT = inferior laryngeal area; TO = hyoid area.

The following table shows the relations between the cutaneous areas and the internal organs:

Area in the Trunk and Limbs.	Area in the Head.
Heart . . C3, C4 – D2 – D8	Ventricles and aorta, N, FN, MO, FT. Auricles FT, T, V, P . .
Lungs . . C3, C4 – D4 – D9	. . N, FN, MO, FT, T, V, P . .
Stomach D7 – D9	. . FN, MO, T, V, P
Intestine D9 – D12	V, P, O
Rectum Sac. 2 – Sac. 4	
Liver . . C3, C4 – D7 – D10	. . FN, MO, T, V, P, O
Gall bladder . . D8 – D9	T, V
Kidney and urethra D11 – L1	
Bladder (mucous membrane and neck) Sac. 3 – Sac. 4	
Detrusor vesicae . D11 – L2	
Prostate . . D10 – D12 Sac. 1 Sac. 3.	
Epididymis . D11 – D12	
Testicle . . D10	O
Ovary . . . D10	O
Ovarian appendix D11 – L1	
Uterus . . D10 – L1	
Neck of uterus Sac. 2 Sac. 4.	
Mammae D4 – D5	
Spleen (from Signorelli) D6	

IV. Of internal sensations summed up under the generic name of "desires," that for food is certainly one of the most important from the teleological point of view, because it is directed to satisfying one of the conditions indispensable to life—the supply of nourishment. In its milder stages this desire is not unpleasant and is even an agreeable feeling, commonly known as "appetite"; when more insistent it becomes painful and oppressive and is known as "hunger."

In most of the higher animals and man appetite and hunger are rhythmical sensations, which do not occur until a certain time after the meal, according to the habits of the individual. In man they are generally felt 5-6 hours after the morning meal, 12 hours after the evening meal. "Regularity of meals," said Beaunis, "causes the sensations of hunger to recur with the precision of clockwork." Change of habit in the hours of meals is able to modify the rhythm of hunger: if the meal is delayed 1-2 hours the appearance of hunger is delayed by a corresponding time.

The degree of hunger varies conspicuously in different individuals, and in relation to age, to the rate of metabolism in different constitutions, in different seasons, different professions, and so on.

Generally speaking, hunger is an unpleasant sensation at the level of the epigastric region, which disappears and is replaced by

a pleasant sensation as the stomach becomes filled by food. But if the satisfaction of the want is delayed the unpleasant sensation increases, and spreads from the epigastrium to the surrounding parts, until sensations of constriction, cramp, and strain are produced throughout the abdominal walls, and located specially in the stomach, oesophagus, pharynx, floor of the mouth, soft palate, parotid region, masticatory muscles, temples, and epicranial aponeurosis, where it assumes the diffuse form of dull headache. In other words, hunger is a complex sensation in which all the organs that function during alimentation and digestion participate more or less distinctly. The discomfort in the epigastric region arising from the cardiac orifice or from the whole stomach is the fundamental feeling in hunger, to which are subsequently added the accessory feelings that come from other parts of the digestive system as a whole and the associated organs and tissues.

All conditions that stimulate general metabolism and increase the loss from the organism—such as muscular exercise, cold air, mountain climate, sea air, convalescence after fever, or the early stages of growth—accentuate the sensations of hunger, which under these conditions becomes proportional to the need of compensation, restoration of the loss, and development of the tissues. All conditions that retard metabolism and diminish loss produce the opposite effect: such are the summer season, sedentary habits, complete muscular inactivity, old age, narcotics (opium, tobacco, cocaine, alcohol).

Under abnormal conditions hunger may reach a morbid level, clinically known as *bulimia*. In this case hunger sets in again 1-2 hours after a meal, and if not satisfied may rapidly produce intense pains in the stomach, dimness of vision, agitation, delirium, fainting. All these symptoms subside after a full meal.

There are also morbid perversions of the sense of hunger, in which appetite for things that are not eatable and are even disgusting, such as earth, clay, ash, coal, straw, hair, and excrement, may be developed.

In most acute febrile diseases, although there is tissue-waste and progressive emaciation, there is also loss of appetite (*anorexia*), and hunger may be replaced by repugnance to food of even the most delicate and tempting kinds, which is due not to abolition but to perversion of the sense of taste. In smokers the acquired need to smoke disappears along with the sense of hunger.

Anorexia is not uncommon in hysterical patients, and in predisposed subjects it may be suggested during hypnosis. In the insane *sitiophobia* (repulsion to food) is frequent, but is then due to delusions and not to absence of the sensation of hunger.

Even in sane people an intense moral emotion, *e.g.* bad news, drives away the feeling of hunger. If the attention is keenly

attracted by an interesting book or intellectual preoccupation with some important problem, the sense of hunger disappears, and the hour of the meal may be forgotten.

The intensity of hunger is not generally proportionate to its duration. It is important to distinguish between the hunger that accompanies forced inanition and that of voluntary fasting. In forced inanition hunger is present from the first in abnormal intensity, and is complicated later on by a peculiar delirium (hunger or starvation delirium) which in recorded cases of shipwrecks assumed a terrible form of acute mania. In voluntary fasts, on the contrary, perhaps from auto-suggestion, the sensation of hunger may be tolerable in the first two days of abstinence, and may decrease and entirely disappear after that. Succi, in one of his many fasts of thirty days which we investigated (Florence, 1889), required a narcotic to allay his hunger only in the first two days; in the remaining twenty-eight he only ingested mineral waters, and showed no sign of suffering. The lawyer, Antonio Viterbi, to avoid the disgrace of execution, resolved to kill himself by starvation: he kept a diary of his fast, and wrote in the last seventeen days, during which he neither ate nor drank, that hunger only lasted one day, reappeared for one short hour on the fifth day, and then disappeared entirely. Thirst, on the contrary, was painful up to two days before death, when it also disappeared. On the eve of his death he wrote the following words:—"I reach the term of my existence with the serenity of a just man. Hunger no longer torments me; thirst has entirely ceased; stomach and intestines are quiet; my head is untroubled, my sight clear. The few remaining moments are flowing gently by like the current of a little stream in a delicious meadow. The lamp is going out for lack of oil."

Thirst, too, is a complicated feeling, located in the first instance at the back of the mouth, whence it spreads and becomes general in proportion as it grows in intensity. It is a sensation of scorching, dryness, and constriction of the throat which spreads over the whole buccal cavity, and is specially associated with a general hyperexcitability, with tachypnea and tachycardia as in fever, hot and fetid breath, and dry, burning skin. At its extreme thirst is more painful than hunger; the craving and anguish—the fate of Tantalus, which is the most appalling the human organism can endure—may induce delirium, which soon brings death in its train.

Thirst increases more rapidly than hunger with the duration of the fast, and becomes even more intense. But here, again, we must distinguish between forced and voluntary abstinence. As we said above, in Viterbi's case thirst was painful and lasted much longer than hunger, but it, too, decreased, and finally disappeared in the last two days of life.

All causes that reduce the high percentage of water in the composition of the body are able to produce the sensation of thirst. The heat of the atmosphere which increases cutaneous and pulmonary perspiration, and muscular exercise which excites secretion of sweat, accentuate thirst. Hydropic effusions, diarrhoea, diabetic polyuria, haemorrhage, etc. promote the desire to drink and produce *polydipsia*. Ingestion of highly spiced or salted foods develops the sensation of thirst by subtracting water from the circulating tissue fluids.

Adipsia or suppression of the sense of thirst is very rare. It is seen in certain serious fevers, and is a fatal symptom, presaging the final exhaustion of the nervous system.

The physiological researches directed towards clearing up the origin of hunger and thirst have not led to any very satisfactory results. It is *a priori* evident that the fundamental internal condition of these sensations must consist in the impoverishment of the circulating fluids by loss of water, which produces a corresponding impoverishment of the tissues. This can be shown experimentally. If artificially prepared nutrient substances are introduced into the veins of a fasting dog, it is possible, according to Schiff, not only to assuage hunger but also to nourish the animal. By means also of intravenous or intraperitoneal transfusion of defibrinated blood, hunger can be relieved in dogs, but the starvation deficit cannot be arrested (Luciani and Bufalini, 1882).

In certain clinical cases in which ingestion of food by the stomach becomes impossible the pangs of hunger may be relieved by nutrient enemata. As regards thirst, Dupuytren caused dogs to run in the sun and then relieved their thirst by intravenous injections of slightly saline water. Schiff repeated this experiment successfully.

But how is it, since they are determined by a general craving of the whole of the tissues of the body, that the sensations of hunger and thirst are localised in the first place to definite regions of the digestive system? Are these sensations central or peripheral in origin? Various physiological theories have been propounded in reply to these questions, all of which appear to us to be insufficient or erroneous. Let us see if it is not possible, on the basis of the facts above discussed, to construct a new theory of hunger and thirst better calculated to satisfy the requirements of scientific criticism.

It is undeniable that hunger and thirst are at the outset true *local sensations*, and that it is only as they become intensified that they spread and assume the complex characters of *general sensations*. This fact in no way contradicts the preceding observation that the fundamental quality of hunger and thirst, on which their teleological value as "desires" depends, is more or less

diffused over the whole of the living tissue elements. In fact, it is conceivable that the sensory nerves of the upper part of the digestive apparatus are peculiarly sensitive to the general effects of deprivation of food and drink in comparison with all other nerves of common sensibility. They are, so to speak, the advanced guard which transmits to the centres a warning of defective nutriment in the tissues by arousing the characteristic sensations of alimentary desires. An analogous fact may be observed in the cutaneous sensory nerves in regard to pain; in these the liminal stimulus that causes pain is normally much lower than that of the sensory nerves of the internal organs. They are the sentinels whose duty it is to defend the entire organism against injurious external agents (mechanical, thermal, and chemical), and to arouse appropriate protective reflexes.

Hunger is therefore specially localised in the stomach for the simple reason that the sensory nerves to the mucous membrane of the latter are the most excitable to deprivation of food. Thirst is specially localised in the pharyngeal and buccal mucous membrane because the sensory nerves to these parts are peculiarly sensitive to lack of water in the circulating fluids of the body.

What condition of the stomach constitutes the peripheral stimulus of the sensation of hunger? It is not the state in which the stomach is empty, because all observations made on patients with a gastric fistula, beginning with the famous Canadian subject studied by Beaumont, show that hunger sets in some time after the stomach has been entirely emptied. Nor does the stimulus consist in exaggerated movements of the stomach, for these are much more active during gastric digestion, and cease almost entirely after the stomach has been emptied. Nor can it consist in excess of hydrochloric acid in the stomach, since it is well known that the contents of an empty stomach are slightly acid, or neutral, or sometimes alkaline. The most acceptable hypothesis is that of Beaumont, who attributes the sense of hunger to *turgor of the gastric mucous membrane*, which increases after the stomach has been emptied, and is due, as Heidenhain showed, to the increased volume of the chief cells of the gastric glands (see Vol. II. Figs. 40, 41, pp. 120, 123). It is possible that the gastric turgescence excites the peripheral endings of the sensory nerves to the mucous membrane; but it seems to us more probable that the excitation depends on the chemical changes in the epithelial protoplasm.

On our theory it is easy to account for the fact that the sensations of hunger only last for a couple of days in a prolonged voluntary fast, as was observed on Succi. In fact it is natural to suppose that inanition, which attacks all the tissues, gradually reduces the turgor of the mucous membrane by diminishing the protoplasm of the epithelial cells that act as a stimulus to hunger.

So, too, it may be held that the peripheral stimulus for thirst consists in the dryness of the mucous membrane of the mouth and pharynx, which causes physico-chemical changes in the epithelia, which again excite the terminations of the corresponding sensory nerves.

By what paths are the peripheral excitations of hunger transmitted to the centres? It has been shown in numerous experiments on fasting animals by Sedillot, Schiff, Longet, and Beaunis that the sensation of hunger persists after section of the vagi in the neck and also below the diaphragm. Brachet (1834), however, on starving a dog for 24 hours saw that section of the vagi, performed after ascertaining that the animal was ready to devour the food presented to it, *ipso facto* arrested the desire to eat. But he took no account of the depressing effects of pain, and did not note how long the inhibition lasted, nor when hunger set in again.

We have recently attempted to repeat Brachet's experiment under more favourable conditions, since it is—so far as we know—unique in the whole literature of physiology. Two young dogs, each weighing 4500 grms., were kept fasting for 24 hours. We then, under chloroform, exposed and dissected out both vagi at the root of the neck, and passed an aseptic thread round them, so that the nerves could easily be drawn out and divided; the edges of the wound were then sewn together. While waiting for the effects of the chloroform to wear off, and to increase hunger, the two dogs operated on were kept in a cage with a trough containing water only. After 48 hours' starvation for the one animal and 72 hours for the other, both vagi were cut, under cocaine, to avoid any pain. Previous to this operation both dogs were very hungry. When shown a bit of meat they eagerly tried to seize it, and snatch it from one's hand. Immediately after the nerves had been divided they ran about the room as vigorously as before; but when meat was offered them, they rejected it, after sniffing and licking it. This condition of absolute loss of appetite began to pass off in the first dog (2 days' starvation) after 40 minutes, in the second (3 days' starvation) after 2 hours. On repeating the test in the succeeding hours, the appetite of both dogs was found to be increasing gradually, until it reached the stage of acute hunger, to judge from the avidity with which the animals devoured meat and bones.

These experiments, which complete the too long neglected work of Brachet, seem by their simplicity to be of no little value to the theory of the genesis of hunger. They show, not (as Brachet thought) that the sensory branches of the vagus are the only means of transmitting the excitations of hunger to the centres, but that they undoubtedly represent the most excitable paths for these impulses. They further prove indirectly that the

afferent fibres of the sympathetic are less excitable to hunger-impulses, and only become active some time after the vagi have been cut, or when on prolonged fasting hunger becomes more acute.

The centres for hunger and thirst are certainly, even if not exclusively, localised in the bulb and pons. This is proved by anencephalous human monsters, which, though they have no cerebrum or cerebellum, utter cries a few hours after birth, make restless movements like normal new-born infants, and like the latter are only stilled when their mouth finds the nipple, which they suck with the same avidity. The renowned "brainless dog" of Goltz also appeared to have sensations of hunger and thirst. At the usual hours for meals its movements were accelerated; it uttered impatient cries, raised itself and put its fore-paws on the bars of the cage. When a dish of milk and big pieces of meat were brought near its nose it lapped and chewed and swallowed with evident satisfaction, like a normal dog.

Schiff opposed to the theory of *local peripheral* origin of hunger and thirst the theory of their *central* origin. Starting from the fact that abstinence from food and drink alters the constitution of the blood, he held that this must directly excite the nervous centres. Local sensations of hunger and thirst are, he says, illusory effects of the state of the centres, according to the general law of the peripheral projection of sensation. Just as the patient has sensations of the amputated limb, so the hungering and thirsting subject feels in the stomach and throat the sensations which really arise centrally.

This hypothesis is fairly met by the fact that hunger can be diminished even by the introduction of non-nutritive matters into the stomach. In times of famine stones, chalk, and indigestible vegetable remains are often eaten. Thirst can be temporarily relieved—*e.g.* in cases of atresia of the oesophagus, by taking a little water into the mouth. Do not these facts prove that such sensations have a local peripheral origin? Even more than these exceptional facts, which are difficult of control, we have at hand, within the reach of every one to verify, a valid argument against Schiff's theory—viz. that the sensation of hunger disappears rapidly on introducing food into the stomach long before it has been digested and absorbed, and therefore before the alteration in the blood, which Schiff held to be the direct stimulus to the centres, can have been corrected. The same may be said of the introduction of beverages and the sensation of thirst, the more so since we know how difficult and slow a process is the absorption of water in the stomach.

To give any experimental basis to Schiff's theory, it would be necessary to prove that the nerve-centres were more excitable to stimuli than the peripheral nerve-endings. Any such attempt,

however, is superfluous, seeing that the exact opposite is upheld by every physiologist: the centres, that is certain parts or nuclei of grey matter, are totally inexcitable to direct stimuli, and have in other parts (as the so-called excitable area of the cerebral cortex) and other nuclei of grey matter, like the nerves along their course, a much higher liminal excitability than that of the peripheral endings of the afferent nerves.

The theory of the central origin of hunger and thirst has thus no advantage over that of its local or peripheral origin, and has no such physiological foundation as would force us to regard it as a necessary complement or integration of the general theory of these sensations.

One objection that seems serious at first sight might be made to the theory of the local origin of hunger. Patients who have successfully undergone almost total extirpation of the stomach do not lose the capacity for feeling hunger; in fact they crave for nutriment in the shape of milk or other foods, preferably liquid, more frequently than normal individuals. This objection, however, disappears when it is remembered that in this operation it is always necessary to leave a greater or less portion of the cardiac region, which probably contains the most sensitive part of the gastric mucous membrane; and that in any case the sensory nerves of the stomach, while normally the most excitable to the stimulus of hunger, are not the only nerves capable of transmitting this impulse to the medulla oblongata. The afferent nerves of the intestinal tract are also capable of the same function, and become active when hunger is intense. Obviously they can convey to the centres the craving for food after an operation of gastrectomy.

V. Just as the alimentary wants are teleologically co-ordinated with the preservation of the individual, so *sexual desire* is correlated with the preservation of the species. This desire is felt vaguely and indefinitely from early childhood; it acquires increasingly definite and localised characteristics; finally it becomes imperative when the genital organs suddenly arrive at maturity, that is at the epoch of puberty. The whole organism then undergoes a crisis: the genital organs become the starting-point of new sensations, till then unknown, which more or less involve the whole nervous system, and are signalised by a pronounced alteration of the intellect, feelings, character, and tastes.

Both in the male and in the female the commencement of sexual maturity is marked by a complex of organic and physiological characteristics in addition to the full development of the genital organs, such as the development of the larynx and change of voice (which becomes deeper, more sonorous, and expressional), the growth of the beard and other hairy appendages, the development of the breasts, appearance of menstruation, etc.

In most animals, other than man, the sexual desire appears with puberty, and is only felt at certain seasons, the periods of "*heat*" or "*rut*." In men, on the contrary, and in the higher apes sexual desire is present at all seasons, from puberty to old age; in women it lasts till the climacteric, when the ovaries cease to function, except in certain cases of retarded sexuality. In animals the female, after fertilisation, obstinately refuses to consort with the male; in the human race and the higher apes the female has no repugnance to sexual intercourse, even after impregnation. This distinction is not, however, absolute. In the domestic animals, in which the two sexes are continually in contact, the periods of sexual excitement are more frequent, and there is, particularly in the male, a tendency to persistence of sexual desire, as in the higher apes and in man. On the other hand, close observation of the human species reveals a periodicity in erotic desire, particularly in women.

The most interesting manifestations of sexual appetite in the higher animals are the struggle of the male to possess the female, and the persistent courting of females in the period of heat to induce them to satisfy the male desire. The male is always the more active; the female is passive, and at first repellent, and only gives way later, when the sexual want is well developed in her too, and the ovule is maturated. According to Darwin, all the gestures and expressive play of affection by which the male seeks to ingratiate himself with the female are directed by sexual desire; but it may be held with Beaunis that they rather aim at increasing the sex impulse in the female, and accelerating the ripening of the ovule, since the love-drama may be observed even in the absence of rivals.

Sex desire is the most powerful motive of human life. Differences of individual temperament, of climate, of social surroundings, of moral and religious education give a different character to the manifestations of this appetite. The crude, brutal desire is nearly always mingled in man with a psychical element, which may attain the noblest heights of love, based not merely on physical attractions but also upon moral and intellectual worth. But if love purifies and ennobles the erotic impulse, it does not calm it, but increases its vigour and intensity by the introduction of psychical factors.

When pushed to a morbid degree, sexual desire may assume the form of *erotomania* or *nymphomania*. The perversions of sex instinct in different forms and degrees, and the still more frequent cases of sexual inversion, belong to psychiatry and forensic medicine.

Here we must confine ourselves to considering the sex want or instinct from an exclusively physiological point of view, and must first determine its origin, that is the internal and external

causes of the excitation which, if transmitted to the centres, produces the consensus of pleasant and voluptuous sensations that finally lead to completion of the sexual act.

The sex impulse is essentially connected with the presence of the male and female germinal elements, the spermatozoon and the ovule. This is the fundamental fact by which the indispensable internal conditions of sexual impulses are determined. Evidence for this is afforded by castration, which as a rule abolishes or checks sexual desire. To this rule there are undeniable exceptions: the Mussulmans accordingly insist that the guardians of their harems shall undergo amputation of the penis as well as the testicles. The exceptional occurrence of erotic erection in castrated persons is probably due to the castration having been performed not in infancy but in advanced childhood or adolescence.

Another interesting fact may be observed in eunuchs. Although they lose the reproductive desire properly so-called, the voluptuous sensations of sexual affection are not wholly abolished, viz. such as are furnished by sight, hearing, the tactile and muscular sense, and the olfactory sense. Owing to these impulses they become enamoured of their charges, and are the more strict as gaolers in proportion as their passions are involved.

We have thus sufficient evidence that the internal conditions of the erotic excitation which arouses sex desire consist in the development and accumulation of the germinal elements in both sexes, but that the internal excitation is constantly associated with external stimulation from the peripheral organs of the special senses, which may persist even after castration.

Animals exhibit practically the same phenomena. Experiments have been made on them to determine the relative importance of the respective senses in regard to sexual desire, and the results are to a large extent applicable to man also.

In the first place there is the work of Lazzaro Spallanzani, who made a great number of experiments on reproduction, particularly on toads and frogs. He observed that during copulation these animals may be pricked, wounded, and mutilated in various ways without loosening the sexual clasp. The following experiment is particularly interesting:[1]—"Finding two toads in copulation I separated them forcibly; I cut off the thighs of the male and put it down near the female; it then embraced her anew. I cut off the hands of a male toad and placed it near a female; as we know, the males use their hands in copulation; it seized the female with its bleeding stumps and did not release her till all the ova were fertilised. On cutting off the head of a male frog in the act of copulation, it did not let go of the female with its arms and hands; it bathed the ova for an hour and three quarters with its seminal fluid, and nearly all of them

[1] Quoted from the Genevan edition of 1876, by Sénébier.

developed into tadpoles. . . ." Two interesting conclusions can be drawn from these experiments:

(*a*) The sexual impulse in toads and frogs is more potent than the most painful sensations these animals can undergo.

(*b*) Removal of the most sensitive parts and of the whole brain, including of course the olfactory and visual organs, does not inhibit the sexual clasp nor interrupt it if already in progress.

Goltz continued Spallanzani's experiments on spawning frogs, and tried in particular to solve three problems:—

Which part of the body of the female exerts the attractive force on the male that leads to copulation? By what sensory paths is the male attracted towards the female and led to copulate? On what part of the nervous system does the persistent muscular contraction by which the male embraces the female depend, and by what paths is this centre excited?

On these points Goltz came to the following conclusions:

(*a*) At the breeding season every part of the body of the female attracts the male. This was proved by a number of curious experiments in which the female was successively deprived of different organs (the ovaries, sense organs, the whole of the skin, etc.) without checking the impulse of the male to copulation. In fact the male will even embrace the dead female.

(*b*) The male is attracted to the female from afar not by one sense, but by all the senses that can come into play. Goltz showed that all the sense organs successively can be removed from different males, without their ceasing to copulate with the female.

(*c*) The centre on which the clasp depends lies in the upper segment of the cord. The activity of this centre is excited by the mechanical cutaneous stimuli of pressure or friction. Goltz proved that the clasp persisted, not only after decapitation, as seen by Spallanzani, but even after transverse section of the cord between the third and fourth vertebra, or after both these operations. If after isolating the thoracic portion, including the three upper vertebrae and the whole thoracic girdle, from the rest of the body in a frog, the skin of the breast and flexor surface of the arms is stroked, the arms will clasp the finger of the operator in a firm clasp which grows stronger if the friction is repeated. If the breast is skinned, or the three dorsal roots which it contains are cut, this reflex spasm no longer takes place.

Tarchanoff continued Goltz' experiments on the frog and succeeded in isolating the stimulus that produces sexual desire in the male; it is due to the tension in the seminal vesicles when the spermatic fluid collects there. While no other mutilation disturbs the copulating male, which persists, as we have seen, after removal of heart, lungs, and testicles, the moment the seminal vesicles are taken away, or merely opened and emptied, the clasp ceases at once, or does not occur if not already begun. On the

other hand, mere dilatation of the vesicle with an indifferent fluid, such as milk, creates the sexual impulse artificially.

Accordingly, in spawning, when the nerve-centres are highly excitable, the impulse that gives rise to sexual desire comes from the dilatation of the seminal vesicles, and is transmitted by the sensory roots. This is the fundamental factor that gives rise in the male to the desire to seek the female and to copulate with her. During copulation, the whole of the senses with their respective nerve-centres are active, and it is necessary to extirpate them all before the clasp can be inhibited.

No doubt much the same process takes place in the higher animals. Every one knows that in mammals, *e.g.* in dogs, the odour guides the male to find the female, and increases the erection of the genital organs due to repletion of the spermatic vesicles; it is more particularly the colour of the secretion from the small glands of the mucous membrane of the vulva of the female that exerts powerful attraction on the male. The other senses are, however, actively involved in different degrees.

As regards the special centres connected in mammals and in man with sexual desire, the cerebellum—according to the theory of Gall, revived by Lussana and of late years by Bunge—is the centre of the reproductive instinct, of physical love or the erotic sense. This theory was effectively put out of court by our experiments on the total extirpation of the cerebellum in dogs. After this operation dogs have, like normal animals, their periods of sexual excitement and all the concomitant erotic phenomena: bitches have periods of *heat*, in which the whole mucous membrane of the genital organs is congested and secretes a viscid, bloody fluid which excites the olfactory sense in the male, whose advances are received with evident pleasure by the female—two, three, or even more suitors being accepted.

On the other hand, Goltz' researches on the effect of successive ablations of the hemispheres proved that sexual desire is diminished with each successive mutilation. But he notes expressly that dogs with a small residue of cerebral cortex still exhibit traces of sexual impulse, since they sniff at the genital organs of other dogs, even if only momentarily. The "brainless dog," on the contrary, never gave the slightest sign of sexual attraction during the eighteen months in which it was under observation. So that there can be no doubt that the centre which is particularly active before and during coitus lies in the fore-brain. But in which portion of it? If it were credible, as some state, that excision of the olfactory lobes and nerves obliterates the sexual impulse in dogs, the question would be solved; but as we have not controlled this assertion we cannot accept it unreservedly.

Broadly speaking, the same facts can be observed in man as

in animals, although in different degrees, inasmuch as they are subordinated to the higher development of the intellect and the evolution of the aesthetic and moral sense.

One further physiological problem must here be taken into consideration. Is the sense of pleasure, which is localised especially in the mucous membrane of the internal genital organs of both sexes, a special modification of the sense of contact, or is it a special sense, served by specific corpuscles or nerve-endings?

Much morphological research has been directed to this subject, but no conclusive solution has at present been reached.

Krause (1866–81) first studied the nerve-endings in the external genital organs of both sexes, and described special corpuscles in the form of end-bulbs, which he termed "genital corpuscles." Of the many other histologists who have studied this subject, Retzius (1876–90), Aronson (1886), Dogiel (1893), Timofeew (1891), and Sfameni (1904) deserve special mention.

Retzius and Aronson, who investigated the skin of the glans penis, clitoris, and vagina of the rabbit, discovered large and small genital corpuscles. They found that the nerve-fibres to these parts divided into fine branches, which ended in knobs.

Dogiel investigated the human genitals as well as those of animals. In addition to Krause's end-bulbs or spherical corpuscles, large and small, he also found Meissner's corpuscles. He further discovered that filaments ran out from Meissner's corpuscles, and terminated in oval cuneiform or pyriform swellings, in the midst of the cells of the deep layers of the epithelium; by these continuity is established between the nerve corpuscles and the epithelial cells. He, moreover, found a nerve network in the epithelium which also reached the more superficial layers, in the formation of which not only the myelinated fibres, but also the fibres non-myelinated from their origin, participated. Timofeew described a special capsulated nerve-ending in the male sexual organs of certain mammals. Two distinct kinds of nerve-fibres penetrate these — one thick and medullated, which lose their myelin sheath as soon as they emerge from the capsular sheath, and then expand into the form of a band with dentellated edges, and terminate at the opposite pole of the ramified or simple, pointed or rounded corpuscle; the other, much finer, which also lose their myelin sheaths, and terminate after branching repeatedly in delicate varicose fibrils which form a network. He confirmed the presence of Pacinian corpuscles on the external genital organs of both sexes, as already described by Schweiger-Seidel, Klein, Rauber, and others.

Sfameni's more recent observations were made upon the genital organs of the cow, sheep, mare, ass, bitch, and woman. In all these species the differences in the nerve-endings are insignificant. In any one animal the different types of corpuscles present an

endless series of transitional forms which pass imperceptibly from the typical Pacinian corpuscle to more elaborate and diffuse nerve-endings. There is accordingly no fundamental difference in their structure, and they can all be referred to the following uniform type: "A nerve-organ, provided with, or destitute of, a sheath of connective tissue, and consisting of one or more nerve-fibres, which after losing their medullary sheath (if myelinated) expand within and around a granular and nucleated substance."

Three points here deserve consideration :—

(*a*) Sfameni neglects the nerve-fibres which are distributed to the epithelium, because they are invisible by the gold chloride method of staining, which he adopted. The intra-papillary nerve-endings show certain small differences between one region



Fig. 27.

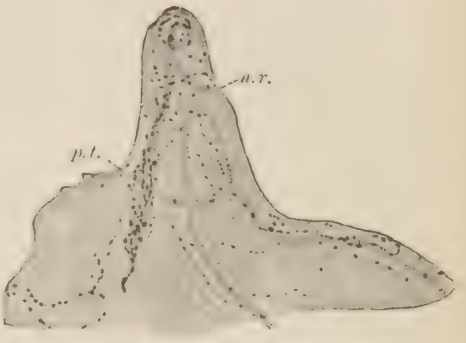


Fig. 28.

Figs. 27 and 28. - Papillae of clitoris of female. (Sfameni.) *n.r.*, granular reticulum; *p.t.*, papillary tuft, the branches of which are lost in the network.

and another; in the clitoris, *e.g.*, there are more nerve elements, and also more elaborate forms of nerve-endings, than in the labia minores. In all cases the papillae are supplied by a double system of myelinated and non-myelinated fibres, which arise in the superficial plexus. Both kinds of fibres expand in the papilla, sometimes in the irregular form of a granulated network (Fig. 27), often in a perfectly regular form which simulates a true end-bulb. In addition to these nerve-endings others may be found which resemble very simple Meissner's corpuscles, as well as forms analogous to the papillary nerve plexus which Ruffini described in the finger-tips (Fig. 28). Within the network certain cellular formations are to be seen, some of which stain with gold chloride almost like the nerve-fibres (Fig. 29), and which can be seen in direct continuity with the nerve network. According to Sfameni, therefore, these must be true nerve-cells, and not connective tissue-cells, as some have asserted.

(*b*) The reticular layer of the cutis contains a great variety of nerve-endings. The simplest and most superficial form is Krause's end-bulb, which Dogiel described minutely, first in the conjunctiva of the eye, and subsequently in the external genital organs of both sexes (Fig. 30). From these more elementary forms of corpuscles there is a gradual transition to other more complex forms, the so-called "genital corpuscles," which Sfameni, like Dogiel, holds to be compound Krause's bulbs (Figs. 31 and 32 show two of the many varieties). The name of genital corpuscles is morphologically a misnomer, because similar forms exist not

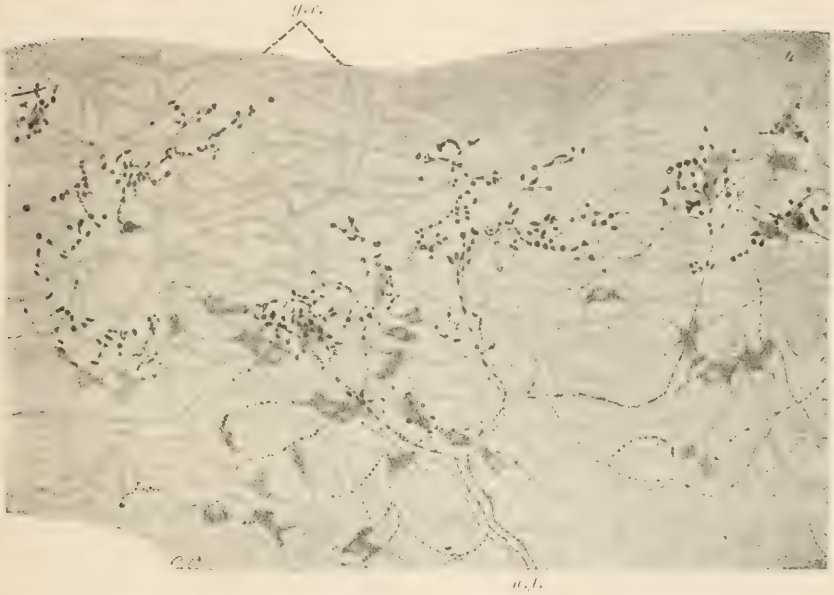


FIG. 29. – Clitoris of sheep. Section oblique to surface. (Sfameni.) *n.f.*, myelinated nerve-fibre; *g.r.*, granular reticulum; *cc*, superficial cells of derma in relation with the granular reticulum.

only in the conjunctiva, but also in the joints. From the so-called genital corpuscles there is a further gradual transition to more elaborate corpuscles, more or less similar to those described by Golgi and Mazzoni, and by Ruffini in the finger-tips. Lastly, there are corpuscles which appear to be transitional forms between Golgi-Mazzoni corpuscles and Pacini's corpuscles. These are largely represented in the female genital organs.

(*c*) There are comparatively few nerve-endings in the loose subcutaneous tissue. Ruffini's end-organs are present in various forms (Figs. 33 and 34), also Pacini's classical corpuscles (Fig. 14) and other related forms, such as the Golgi-Mazzoni corpuscles, which here are usually smaller than those shown in Figs. 10, 11, 12.

The general morphological conclusions of Sfameni from his own observations and those of Dogiel upon the genital organs are shown in his diagram (Fig. 35).

Without pausing to discuss and analyse the hypothesis, by which, according to Sfameni, the different nerve corpuscles are to be regarded as small peripheral ganglia (analogous to the spinal ganglia), the function of which is to modify the nervous excitations that reach them by way of the true nerve-endings (the intra-dermal and intra-epithelial fibres), we will confine ourselves to stating that according to Sfameni the whole of the nervous apparatus which he represents must be the substrate not only of the male and female genital organs, but of the organ of tactile sense in general. Consequently, the anatomists who follow Sfameni neglect all the physiological evidence, and arrive at a theory which is wholly contrary to that which physiologists have adopted from minute researches into the different modalities of sensation at distinct parts of the body-surface. The skin, in which physiologists distinguish *four* different senses, possesses, according to Sfameni, only *one* of the five senses recognised by physiology from all time, *i.e.* tactile sensibility. This enormous disparity proves the vast superiority of physiological methods of research over the anatomical methods of analysis of the sense-organs.



FIG. 30.—Krause's club, from mucous membrane of vulva of bitch. (Sfameni.) *n.f.*, myelinated nerve-fibre; *g.s.*, granulated substance; *c.s.*, connective sheath.

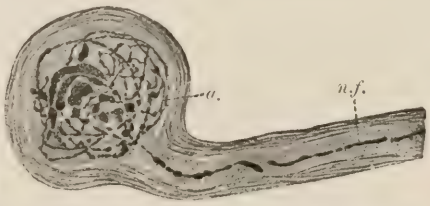


FIG. 31.—Spherical genital corpuscle from female clitoris. (Sfameni.) *n.f.*, myelinated nerve-fibre; *a.*, axonal network.

The topography of the different kinds of sensibility in the human penis was studied by v. Frey. One of the most important facts which he discovered is that the gland of the penis has no

true touch spots. On exciting with pointed mechanical stimuli an exceptionally high threshold of excitation is found, corre-



FIG. 32.—Compound genital corpuscle from labia minores. (Sfameni.) *b.c.*, blood capillaries; *a.* axonal network; *c.s.*, connective tissue sheath.

sponding to that of pain, but not to that of contact, which is normally much lower.

At the root of the penis the touch spots become less



FIG. 33.—Cylindrical Ruffini's corpuscle, from labia minores. (Sfameni.) *n.f.* myelinated nerve-fibre; *e.c.s.*, elastic connective sheath, surrounding granular substance.

frequent; they are more abundant as the border of the prepuce is reached; on the internal surface of the prepuce, which covers the gland, they diminish gradually and disappear. The

frenulum is rich in touch spots. Mechanical excitations of the gland which move the whole penis can be transmitted to and perceived by the tactile points of the frenulum and prepuce; but if the gland is pinched without moving the penis, it is seen that slight pressures are not noticed, and strong pressures produce pain. At the edge of the prepuce, on the contrary, and on the frenulum, a slight pinch does give a sensation of contact, and a stronger pinch causes pain. Corresponding results are obtained with faradic stimulation. The pain produced in the gland is different in character from that felt in the prepuce and the skin in general: it is a tearing and cutting pain, which seems to arise deeper down.



FIG. 34.—Globular Ruffini's corpuscle, from labia minores. (Stameni.) *n.f.*, myelinated nerve-fibre; *e.c.s.*, elastic sheath of connective tissue; *a.e.*, axonal expansion; *s.f.*, sympathetic fibre.

The thermal sense also presents certain peculiarities in the human penis. The number of thermal points for heat and cold increases like the pressure points from the roots of the penis to the edge of the prepuce; but in descending along the inner surface of the prepuce to the root of the gland thermal sensibility increases instead of diminishing. The corona is one of the regions in which thermal sensibility to cold is most intense (as in the tips of the mammae, the eyelids, lips, and tongue). Passing from the corona towards the mouth of the urethra, this sensibility rapidly diminishes and disappears. The frenulum and meatus alone contain many cold points.

The cold spots of the gland react to adequate stimuli as well as to faradic stimuli. They also show the phenomenon of paradoxical excitation in a remarkably acute form. Stimulation of the cold spots with the end of a heated metal cone produces an indubitable sensation of cold, which increases as the temperature of the cone is raised above the mean temperature of the body. Above 50° C., however, a sensation of burning heat is associated with that of cold. Owing to the great number of cold spots in the corona, the contact of hot metal surfaces also produces a sensation of cold that is more intense within physiological limits in proportion as the temperature of the stimulating body is raised. It is only around the mouth of the urethra that the heat stimulus produces a sensation of warmth. Determination of

the heat spots is therefore rendered very difficult by the number of cold spots present.

Apart from thermal and pain sensibility in the gland, and pressure sensibility in the prepuce, frenulum, and skin of the



FIG. 35.—Diagram of terminal nerve apparatus in female genitals, corresponding, according to Sfameni, with the end-organs of tactile sensibility in general. The tactile organ is supplied by myelinated (*f.n.*, *f.n.'*, *f.n.'''*) and non-myelinated (*f.s.*, *f.s.'*, *f.f.s.*) fibres. The first form a network with large branches and nodosities (*r.g.*); the second, a network with wide meshes and fine ramifications (*r.s.*). These networks are found together in the epithelial and sub-epithelial layers. The branches of the first (*r.g.*) come into contact with differentiated cellular elements (*r.t.*): peripheral sensory cells. Some fibres, both myelinated and non-myelinated, do not run direct to the periphery to enter the corresponding network, but contribute on the way to the structure of one or more end-corpuscles, which they leave as ultra-terminal or, better, ultra-corpuscular fibrils (*f.u.*, *f.u.'*). In each corpuscle there are two nerve-endings: one, primary (*t.p.*), comes from the large myelinated spinal fibres (*f.n.*, *f.n.''*); the other, secondary (*t.s.*), from the sympathetic fibres (*f.n.''*, *f.s.*).

penis, v. Frey found no sensory points reacting to any other quality of sensation.

There is accordingly no foundation for the view by which some have sought to define a special sense on the outer surface of the genital organs for voluptuous pleasure. Excitation of the tactile points, and perhaps also of the pain points and thermal points of the penis, may certainly be associated with voluptuous sensations

such as occur in other special regions of the skin and other mucous membranes. But this association is neither constant nor necessary, and probably depends on the summation of particular conditions of excitability in the sensory centres.

VI. In the group of *functional sensations*, that is the sensations that accompany the various functions of the internal organs, a peculiar importance, both from the physiological and from the psychological point of view, attaches to the sensations by which we become aware, directly or indirectly, of the state of the muscles, the modes and different degrees of their functional activity, and the changes, generally speaking, in the active and passive organs of the motor system. It is by the sum of the sensations arising from the motor system that we are able to control our movements, and to carry them out with the necessary precision.

The character of these sensations is always vague and ill-defined. The slight degree of tension normally present in inactive muscle, on which muscular tone depends, certainly lies below the threshold of consciousness. We are able without hesitation to call up the exact degree of muscular contraction necessary to reach a given aim, *e.g.* to produce a musical note of a certain pitch. This means that we have, unconsciously, an exact notion of the degree of tension present in the vocal muscles previous to their voluntary contraction.

The sensations of tension and resistance that accompany the state of contraction and the contractile movement of the muscles are obscurely perceived.

With the eyes blindfolded or in total darkness, we are conscious of a certain position in which we place, say, an arm; we are able to describe it, and even to imitate and reproduce it exactly with the other arm. We are aware of the changes of movement of the arm, whether these are made voluntarily or passively.

When we lift a weight, or in an active movement meet with an obstacle or a resistance imposed by a body external to the limb, we are able to apprehend the degree of effort exerted in raising the object or removing it. The estimation we make of our sensations of tension and resistance, and of the force required to overcome them, are, as we shall see, the most important elements in the judgment we form of the weight of objects.

These and other more obscure, less well defined, and poorly localised bodily sensations which accompany functional activity of the motor organs in animal life are collected by the majority of physiologists into one category known as the *muscular sensations*.

This term is inappropriate, and must be rejected as erroneous if it is taken to mean that all the different varieties of sensations which it comprises originate from specific sensory elements contained in the muscles; for we reason experimentally that most of

them lie in the tendons or tendinous sheaths, the fascia, and the surfaces of the joints. So that the term "muscular sensations" is justifiable only if we admit, with Sherrington, that it covers the sum of the sensations which originate in the motor apparatus, that is, in the muscles and accessory organs of movement.

Various theories of the nature and origin of these sensations have been put forward, which we will next examine one by one, this being the best way to discuss the whole subject and its significance.

It is evident that the sensations that originate in the active state of the muscles are intimately mingled with the cutaneous sensations of contact or pressure. When a muscle contracts, the soft parts are displaced, so that the skin relaxes and forms folds in certain regions, while in others it becomes tense. The relaxation or tension of the skin, and the rapidity with which it occurs, are proportional to the extent, rapidity, and duration of the movement or contraction of the muscle. So that the sensations aroused by means of the tactile cutaneous nerves are able to inform us of the energy, speed, and duration of the muscular contraction.

On the strength of this fact, and in view of the delicacy of cutaneous sensibility, certain physiologists, including M. Schiff (1855), Lotze, Hansen, and Auber, assumed that in explaining the origin of the so-called muscular sensations it was unnecessary to recognise the existence of a specific peripheral sensory apparatus, with special afferent nerves, located in the organs of movement, inasmuch as they were adequately aroused by excitation of the tactile cutaneous nerves which inevitably takes place whenever the muscles become active.

But even if we admit the more or less appreciable intervention of cutaneous sensation during the activity of the muscles, it can easily be demonstrated that this is not sufficient to explain the whole of the phenomena included under the term "muscular sensations."

In the frog it is possible to suppress the whole of the sensations that are cutaneous in origin by removing the skin from the four legs without perceptibly affecting the regularity of the customary movements of walking, jumping, and swimming. This is Cl. Bernard's experiment, which proves that the regularity of the frog's movements is independent of any possible controlling action by the cutaneous sensations, making it highly probable that the controlling action depends fundamentally upon sensations transmitted directly from the muscles or indirectly from the passive organs of the motor system.

For the true solution of the question it is necessary to take into consideration the phenomena observed on man in cases of pathological alterations of cutaneous and muscular sensibility.

Neuropathology presents many such cases. Anaesthesias of hysterical origin, those of traumatic neurosis, and those observed in syringomyelia are comparatively common. These patients sometimes retain the power of carrying out all movements with the affected limbs in a normal or almost normal manner, so long as their eyes are open. But when the eyes are shut they lose consciousness of the movements they are making, and are unable to describe the position actively or passively taken up by the anaesthetic limb. These cases are difficult to interpret. It may be thought that the anaesthesia is confined to the cutaneous nerves, and that this, on Schiff's theory, involves loss of muscular consciousness (Magnin, Oley, and others). But more probably the defect depends on abolition or suspension of both cutaneous and muscular sensibility (Beaunis and others).

This is apparent from a case described by Strümpell (1902) of total paralysis of every kind of sensation in the forearm and right hand, with complete preservation of motility, in a patient who received a knife-wound in the cervical spine which probably cut through the grey matter of the dorsal horn and the lateral portion of the right dorsal column. The injury was followed by a complicated illness with widespread symptoms; but when the wound healed after about nine months, all the symptoms were confined to the right upper limb. With closed eyes the patient was unable to say whether the fingers of his hand were flexed or open, or to maintain it in any posture in which he was placed with his eyes open (Figs. 36 and 37). Under the control of vision he was able to exert a strong pressure with his hand and to place the fingers in any position; with shut eyes he was incapable of carrying out any definite, complicated movement with that hand, or of extending or flexing it at command.

This is a clear demonstration that the abolition of superficial and deep sensibility in the hand and forearm renders the patient incapable, without the use of his eyes, of accurate sensation either of the position or of the active and passive movements of the hand or fingers.

From our standpoint cases of well-authenticated dissociation of superficial and deep sensibility are more interesting. Clinical cases have been well described, in which the sensibility of the deep tissues was wholly or partly retained, while cutaneous sensibility was entirely abolished. In a hysteric described by Duchenne (Boulogne) there was total insensibility of the left upper limb (analgesia, anaesthesia, insensibility of muscles to electrical and mechanical stimuli), although the patient, even with closed eyes, was aware of the active and passive movements of the limb, could estimate the weight of objects placed in the hand, and did not let them drop, proving, according to Duchenne, that the sensibility of the articular tissues persisted.

Two patients described by Landry exhibited diametrically opposite phenomena of dissociation: tactile and pain sensibility of the skin on one side were retained, while the sensibility of



Fig. 36.

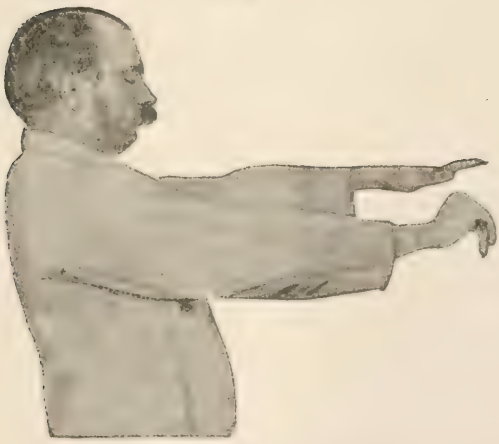


Fig. 37.

Figs. 36 and 37.—Strumpell's patient, who suffered from complete loss of superficial and deep sensibility of right arm. With eyes open he was able to place and maintain both hands in the same position; with eyes shut he involuntarily altered the position of the right hand—as shown in the photographs.

the deep tissues was completely abolished. In these cases, as soon as vision was excluded, the patients lost consciousness of the position of their limbs, and were no longer able to appreciate either active or passive movements.

Not a few other similar cases have been described by neuropathologists; but in the majority of them the loss of deep sensibility was incomplete, or was associated with a slight disturbance of superficial sensibility.

In proof of the secondary importance of superficial sensibility as compared with that of the muscles and the deep tissues in general, we may refer to the experiment of Beaunis (1887) on the function of the laryngeal muscles. After anaesthetising the mucous membrane of the glottis of a tenor by the application of cocaine, which also made it pale owing to vascular constriction, he found that the intonation of the voice, that is, the exact formation of the separate musical notes, was not appreciably altered; the purity and *timbre* of the sounds alone seemed somewhat affected, which might be due to the altered blood-supply of the organ. The conclusion drawn by Beaunis seems satisfactory, that "muscular sensibility plays the leading part in the tension of the vocal cords by which accuracy of tone is determined, and the sensibility of the mucous membrane only intervenes, if at all, in a purely secondary manner."

We have consequently sufficient evidence for assuming that the muscular sensations which depend on specific sense organs situated in the muscles, tendons, joints, and accessory organs of the motor system are independent of the sensations of the skin and adjacent mucous membrane.

The founders of the theory of muscular sense as a sixth sense were Charles Bell (1832) and Panizza (1834) (see Vol. III. p. 467). They founded their entire theory on the phenomena of the disorganised movements of the limbs obtained after section of the dorsal roots (root ataxy).

E. H. Weber (1846) developed the theory of a sense by which we become aware of the degree of muscular effort necessary to overcome the resistance that opposes our movements, and gave it the name of sense of effort (*Kraftsinn*). He succeeded by ingenious experiments in demonstrating that we are able to appreciate the difference between two weights far more exactly by this sense than by tactile or pressure sensibility. By sensations of pressure alone, such as those produced by weights upon the fingers resting supinely upon a support, the difference in weights which are as 29 : 30 can be perceived. When the muscle sense is employed, as in raising with the fingers a pan on which the weights are placed, we are able to distinguish them when the values are in the ratio of 39 : 40. In this case (according to Weber) the lower threshold of difference does not depend on the association of tactile and muscular sensations, because in judging of the weights raised we entirely neglect the sensation of pressure of which we are aware in the hand that supports the scale-pan. In fact our judgment does not alter when we voluntarily increase

this pressure beyond what is strictly necessary to sustain the weights.

Anatomical proof that the muscles, tendons, and joints are sensitive, owing not only to the sensory nerves that traverse them to reach the skin, but also to the fibres that terminate there, was given by Reichert, Kölliker, and others.

According to Kölliker the sensory nerve-fibres of muscles almost always run towards the surface and ends of the muscle, and terminate in the connective tissue, perimysium, and tendons, never in the sarcolemma of the muscle-fibres.

Rauber (1883) and Ciaccio



Fig. 38.—Modified Pacinian corpuscle of cat. (Ruffini.)



Fig. 39.—Pacinian corpuscle of rabbit, modified so as to resemble the club-shaped corpuscles of Golgi-Mazzoni. (Ruffini.)

(1889) first described in the muscle sheaths, tendinous sheaths, and joint capsules, nerve-endings resembling Pacinian corpuscles, of various forms and sizes, which differ slightly from those of the subcutaneous connective tissues. A more minute description of their conformation, topography, and relations was afterwards (1897) given by Sherrington and Ruffini (Figs. 38, 39).

Kölliker (1862) and Kühne (1863) discovered among the ordinary muscle-fibres characteristic bundles containing a few

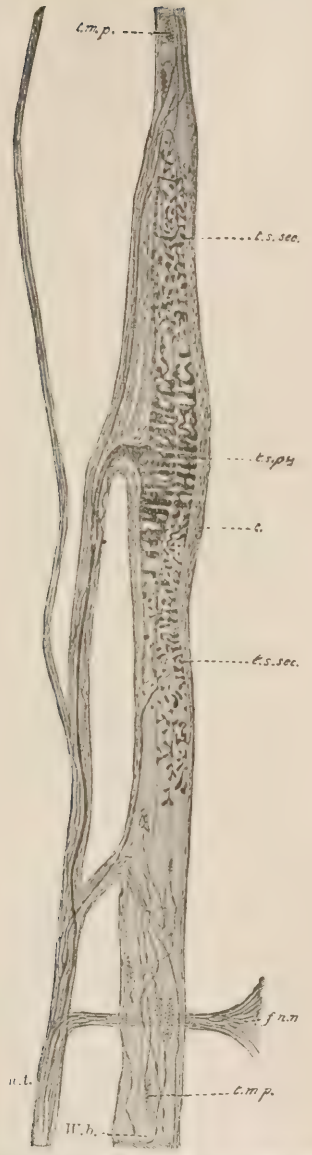


FIG. 40. Semi-diagrammatic representation of neuro-muscular spindle from adult cat to show complex nerve-endings. (Ruffini.) *c.*, capsule; *n.t.*, nerve-trunk; *W.b.*, Weissmann's bundle; *n.m.s.*, nerve-fibres ending in the muscle bundles that surround the neuro-muscular spindle; *t.m.p.*, motor end-plates (after Cipollone); *t.s.pr.*, primary sensory endings; *t.s.sec.*, secondary sensory endings.

muscle-fibres of embryonic appearance, invested by a sheath, similar to that of the Pacinian corpuscles, which assumed a spindle form at the point of entrance of the nerve, and were therefore called nerve-muscle spindles. According to A. Cattaneo and Kölliker they are usually found near the tendinous ends of the muscles; but Sherrington and Ruffini found numbers of them also in the fleshy parts of the muscles. A minute anatomical description of the neuro-muscular spindles, and particularly of the different modes in which the nerves terminate in them, was first given by Ruffini (1892–98). Here we can only reproduce one of the most characteristic figures which he observed on the cat (Fig. 40).

The sensory nature of the nerve-muscle spindles was recognised by Körschner (1888) and Ruffini (1892), and experimentally demonstrated by Sherrington (1894). He saw that the myelinated nerve-fibres of the spindles underwent no change after section of the ventral spinal roots, and concluded that they originated in the cells of the dorsal root-ganglia. Cipollone (1898) by other ingenious experiments showed that the fine medullated fibres of the spindles as well as the end-plates connected with them are *motor* fibres and endings, while the large medullated fibres and the plentiful primary and secondary endings of the fusiform swelling are *sensory* fibres and endings. In rabbits the first degenerate, the second remain perfectly intact, when necrosis of the grey matter and root cells of the lumbar cord is produced by Stenson's method, while the cells of the

corresponding spinal ganglia and the peripheral sensory nerves remain intact.

A third nerve end-organ was discovered by Golgi (1880) in both man and the higher vertebrates in the transitional region between the tendons and the muscle-fibres, and is known as the musculo-tendinous organ or corpuscle. Such organs were found by Marchi in the tendons of the eye-muscles (1881), and were studied in closer anatomical detail by A. Cattaneo (1888). For the most part they are fusiform, sometimes cylindrical, bodies of different sizes with a smaller tendinous end turned towards the insertion of the tendon, and a larger muscular end turned towards the belly of the muscle. We cannot enter into their structure, which is plainly shown in Figs. 41, 42, and 43, taken from Cattaneo and Ruffini.

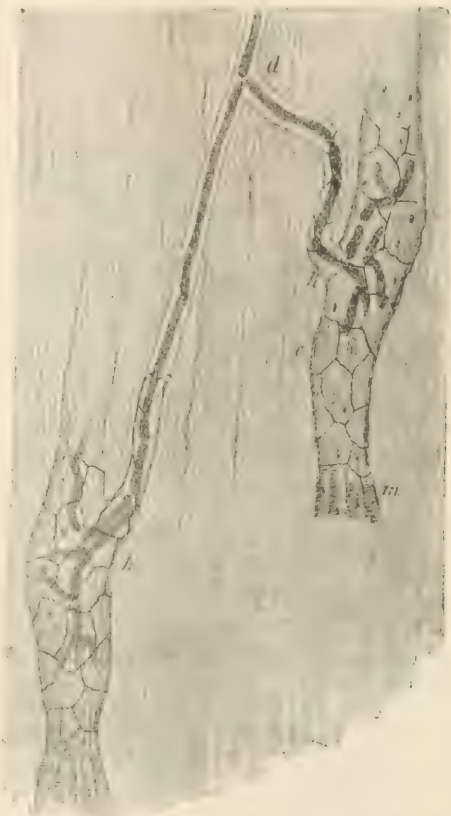


FIG. 41. Two musculo-tendinous organs of rabbits, treated with silver nitrate and osmic acid, enlarged about 100 diameters. (A. Cattaneo.) *d*, bifurcation point of a fibre that innervates two organs of Golgi; *e*, endothelium investing this organ; *h*, Henle's sheath, which the nerve loses on entering the corpuscle; *m*, muscle bundle united with the small tendon of the organ of Golgi.

The sensory nerves and nerve-endings of the joints have been less studied anatomically, although clinical experience has proved their extreme sensibility in cases of inflammation. The articular cartilages seem to be destitute of nerves, but these are abundant in the ends of the bones, the periosteum, articular ligaments, and synovial capsules. Rauber found more or less modified Pacinian corpuscles in the vicinity of nearly all the joints; it is not yet known whether Golgi's organs are also present there.

It follows from the preceding discussion that the active and passive organs of movement are supplied with sensory fibres that have three special end-organs, the modified Pacinian corpuscles, the musculo-tendinous organs of Golgi, and the neuro-muscular

spindles. Many ingenious deductions have been made from the structure or topography of these three organs with a view to determining their respective functions as organs of the muscular sense.

The conclusions of Cipollone and of Sherrington seem to be of special importance. After Cipollone's demonstration of motor

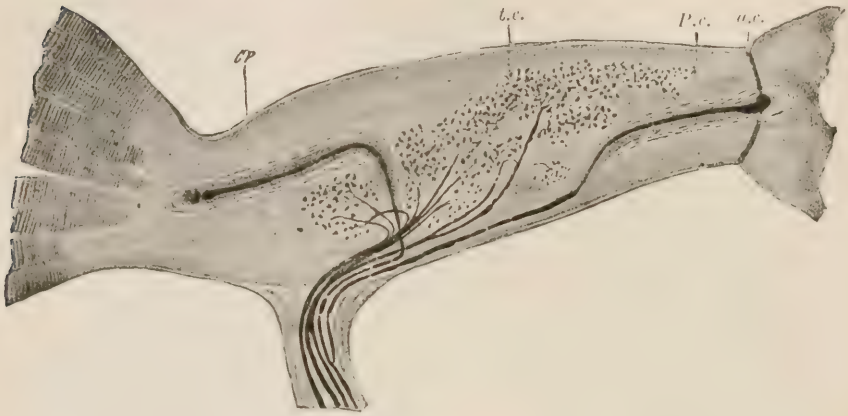


FIG. 42.

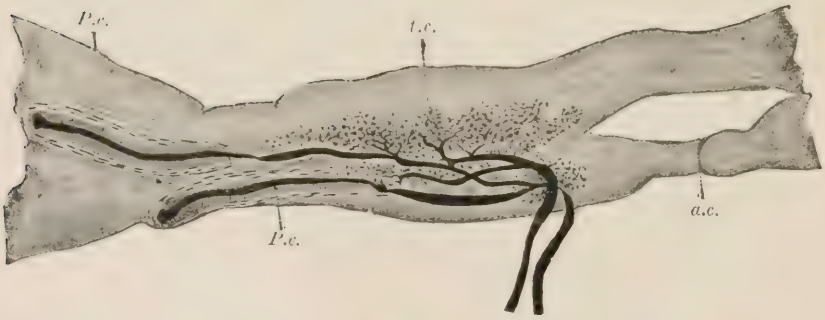


FIG. 43.

FIGS. 42 and 43.—Two musculo-tendinous organs from cat, each containing two modified Pacinian corpuscles. (Ruffini.) *t.c.*, terminal nerve expansion belonging to musculo-tendinous organ; *P.c.*, modified Pacinian corpuscle; *a.c.*, annular constriction (A. Cattaneo), or small strip of connective tissue (Ciaccio).

nerve-endings in the neuro-muscular spindles, there could be no doubt that the special muscle-fibres which they contain contract during the excitation transmitted by the motor nerves, and in contracting mechanically excite the ring-shaped and spiral sensory nerve-endings by which they are surrounded. The more or less appreciable sensations which they arouse in the central nervous system are proportional in intensity to the degree

in change of form of the spindles. In a word, they function as *isotonic dynamometers*, by which the centres become aware of the degree of active contraction of the muscle and perhaps also of the degree of passive traction to which it is subjected by the action of the antagonist muscles. This hypothesis seems to us simpler and more acceptable than that of other authors who maintain that the sensitive ends of the spindles are excited by the action-current developed in the muscle, or by the molecular chemical changes that take place in it during the contraction.

While the sensory nerve-endings in the spindles are in direct relation with the muscle fibres, and the stimulus to which they react is given by the form changes of the muscle, the sensory endings in the organs of Golgi are in relation with the tendinous fibres, and the mechanical stimulus to which they react is produced by the tension they are subjected to in consequence of the active state of the muscle. While the former function as *isotonic dynamometers*, the latter function as *isometric dynamometers*—that is, they signal to the centres the tension changes, rather than the form changes of the muscle. For the due performance of this function it is unnecessary to predicate any extensibility of the tendinous organs of Golgi, as was assumed by Cipollone. In fact, if they were extensible their isometric signals would be incorrect.

According to Marchi, the muscles of the eye-ball contain no other sensory organs capable of signalling the delicate antagonism of their functions, which proves that the musculo-tendinous organs must be able to send intelligence of the least traction exerted by these muscles.

To explain this great sensibility of the organs of Golgi, Cipollone happily takes into consideration their curved form and oblique position in respect of the tendinous fascia, and the occasionally undulating course of the tendinous fibrils of which they consist. It is evident that, under these conditions, the tendinous organs of Golgi can be affected even by the weak traction exerted on them by the muscle; there is no real increase in their length, but an adjustment of the fibres that run curved, undulating or obliquely to the line of traction of the muscle. This adjustment or displacement may be accepted as a stimulus adequate to excite the nerve-endings mechanically.

As regards the functional value of the modified Pacinian organs present in the motor system, particularly in the tendons, bones, and articular tissues in general, Sherrington correctly points out that they are by their position, and particularly from their structure, eminently suited to signal the different degrees of compression that occur during the changes of relation of the articular surfaces, whether these are actively produced or passively imposed.

Which of these three different sensory organs located in the

muscles, tendons, and articular tissues has the greatest physiological importance in arousing the so-called *muscular sensations* by which movements are controlled? In this connection some interesting physiological and clinical observations may be cited.

Certain early observations of Haller and Bichat, confirmed later by Schiff, Bernstein, and others, show that the muscles and tendons are insensitive to many mechanical, thermal, chemical, and electrical stimuli which are effective in other tissues. Sherrington, however, showed that the tendons may be the starting-point of reflexes. Compression of the tendon of the tibialis anticus of the cat invariably produces a reflex in the adductor femoris. Reflexes can be obtained from other muscles. On pinching the muscles of a curarised rabbit, Kleen obtained a fall of arterial pressure. Before that, Sachs obtained reflex convulsions in a strychninised frog, by exciting the central stump of a nerve to the sartorius. Sherrington showed that the knee-jerk phenomenon may be reflexly inhibited by compressing or otherwise stimulating one of the leg-muscles. He also saw that the sudden relaxation of a muscle passively pulled on often discharges a reflex in some other muscle: that the direct stimulation of the muscular nerves gives rise to vascular reflexes, often also to alterations of respiratory rhythm; produces antagonistic effects (by lowering muscle tone) in other groups of muscles; causes decerebrate rigidity to disappear; and finally may induce reflex contraction of other muscles. From these facts we may conclude that the more or less appreciable sensations aroused by excitation of the sensory nerve organs of the tendons and muscles are not unimportant to the regulation of movements.

Other facts, however, indicate that the muscular sensations due to excitation of the afferent nerves of the tendons and muscles remain, under normal conditions, almost entirely below the threshold of consciousness, and are only of negligible, certainly only of secondary importance, as factors in the complex sensations that accompany voluntary movements; and that greater importance attaches, on the contrary, to the excitations arising from the afferent nerves of the articular tissues. This theory was maintained by Rauber, Duchenne, and Lewinski, more particularly on the strength of clinical observations, and was more fully developed by Goldscheider (1889) on the basis of accurate experimental research.

It seems *a priori* probable that the sensibility of the articular tissues as a whole should be of predominating importance in the genesis of the sensations by which movements are reflexly regulated. Every change in the relations between two articular surfaces corresponds to a simple movement, while there is perhaps no muscle that takes part in a single movement only, nor any movement that is not the result of the associated and variously

graduated action of several muscles. Owing to their simplicity the force, amplitude, and direction of the movements of the joints is readily appreciated; the simultaneous contraction of several muscles, on the contrary, can arouse no compound resultant sensation unless there is a separate consciousness of the difference in intensity of the single elementary components of the sensation and their associations.

In the clinical case described by Strümpell (p. 90, Figs. 36, 37) the loss of the sensations of posture and of active and passive movement in the right hand depended not on paralysis of the muscles and tendons, but on the insensibility of the joints. In fact, in Duchenne's case (p. 90), where there was loss of cutaneous and muscular sensibility in the left upper limb, while articular sensibility persisted, the patient was aware of the posture and of active and passive movement.

Lewinski (1879) had under observation an ataxic patient who in standing erect and walking felt as if his right knee were turned in (as in *genu varum*), and was obliged to look to convince himself that it was straight like the left knee, but when he lay down in the horizontal posture the illusory sensation ceased. As the sensibility of the skin and muscles was the same on both sides of the leg, Lewinski concluded that the anomalous sensation was due to a diminution of sensibility on the inner side of the joint. Under ordinary conditions, the sensation in standing, excited by the weight of the body, is uniformly distributed over the whole surface of the joint; when sensation is defective or absent on the inner surface the patient feels as if both articular surfaces of the knee were compressed on the outer side, and were not in contact on the inner side, as if the leg were bent outwards, making an angle that opened externally. The anomalous sensation disappears in the horizontal posture because the cutaneous tactile sensations correct the illusion and supplement the defect in articular sensibility.

Lewinski further saw that if passive movements were executed at different joints on this ataxic patient he only became aware of them when the surfaces of the joints were pressed strongly one against the other. From this he concludes that there is no doubt that sensations of posture depend exclusively on the compression of the two articular surfaces, and sensations of passive movement on the constantly changing points on those surfaces that are compressed during the changes in the relation of the articular heads.

The important experiments of Goldscheider further support this theory. He caused his limbs to be moved passively, and recorded on an apparatus the speed of the movements and their angular value. He found that in many joints quite small movements, frequently less than one degree (0·72 – 0·22), could be appreciated.

According to Goldscheider, the speed of the movement is important, as well as its amplitude. A movement that was imperceptible but close to the threshold of excitation became appreciable when its velocity was increased. It is possible also to establish numerical relations between the two main factors of the passive movements. The liminal speed, that is the minimal degree of angular movement per second, varies in the different articulations from about 0°·25 to 1°·4.

Goldscheider holds that the perceptions of posture and of passive movement depend fundamentally on the deep sensibility of the articulations. Not only are vision and touch not indispensable to them, but the sensibility of the muscles and tendons are of no appreciable importance: the minimal angle of excursion necessary to give the perception of the passive movement remains the same, whatever the initial posture of the articulation. Again, the result does not alter after the skin of the limb has been anaesthetised by electricity: when the cutaneous sense of pressure on the skin is thus eliminated, perception becomes more acute. When, on the other hand, the joints are made insensitive, the perception of movement becomes blunted, and the movements must be of a wider range to be appreciable.

Hence, according to Goldscheider, the articular surfaces are the exclusive starting-point of the sensations by means of which we directly perceive the passive movements of our limbs.

Of course the perception of active movements also depends upon the compressions and excursions of the articular surfaces: but other factors intervene here—the tension of the tendons, and probably also the changes in form of the active muscles, besides the passive traction of antagonist tendons and muscles. In fact, according to Goldscheider, the sensibility to active movements is more delicate than to passive movements, although the difference is not very large.

VII. The discussion of the sensory phenomena connected with active voluntary movements would be inadequate and incomplete if we did not take another important factor into account. Besides the more or less obscurely appreciated sensations which accompany movement, and which are aroused at the periphery by excitation of the terminal sensory organs of the articular tissues, tendons, and muscles—which we have considered under the general name of *muscular sense*,—we have to consider the *central sensation* that precedes the movement, which coincides with the volitional act and gives rise to the efferent current along the motor paths. Johannes Müller, Helmholtz, Wundt, Bain, to cite only the most eminent authorities, maintain that we have not only a sensation of the movement executed, but also a sensation of the movement willed; that the sensation of the active movement is directly associated with motor innervation; that we perceive the intention

before the fact; that the idea of the contraction precedes and does not follow the movement.

But this theory of a *central sense of innervation*, as opposed to that of the *peripheral muscular sense*, finds no supporters in view of the progress and development of the theory discussed above. Some physiologists still maintain that in all voluntary acts a central feeling of innervation is associated with the multiple peripheral sensations; the majority, however, deny Bain's theory even in this restricted form, and maintain that the *sense of effort* results exclusively from a consensus of afferent elementary sensations. We must weigh the arguments for and against the two theories before deciding in favour of one or the other:—

(*a*) Certain phenomena observed on paralysed patients were formerly adduced in favour of the central sense of innervation. If a paralysed person is invited to make a movement with his paralysed limb he puts out all his force without success, and is fully conscious of the effort he makes, although this cannot depend on any excitation from the peripheral organs of the paralysed limb. But it is obvious that this and other similar arguments adduced in support of the theory of an innervating sense are of little value. It has in fact been pointed out by Vulpian and others that when the paralysed person attempts to move the paralysed limb, he throws into action a number of non-paralysed muscles in other regions, and the sensation of effort felt may be due to the movements performed by these muscles.

(*b*) If the sensation that accompanies the movement were due solely to peripheral excitations, there would, according to Wundt, be perfect parallelism between the sensation and the muscular contraction. But, as a matter of fact, we know by experience that the sensation does not depend principally on the extent of the movement effectively carried out, but on the force of the impulse that emanates from the motor centre. In proof of this we may cite the fact described by Delboeuf. If any one repeatedly exerts the whole force of his hand on a spring dynameter, he has the illusory sensation of using the same effort each time, and is surprised to see the rapidly decreasing values in a series of ten or twelve efforts. There is evidently no parallelism here between the sensation of effort, which remains uniform, and the movement actually carried out, which rapidly decreases. So that we may conclude that the first is central in origin and does not depend on the second.

(*c*) Weir-Mitchell argued in favour of a central sense of innervation from the illusory phenomena observed after amputations, of which he made an exhaustive study from over 100 patients. It has been known since the time of Johannes Müller that nearly all persons whose limbs have been amputated (94 in 100) have the illusion that the lost limb is still in its place, and though this feeling

may be vague or disappear it is readily called up again by any influence affecting the stump (Vol. III. p. 201). Weir-Mitchell shows that the illusion of the presence of the lost limb is persistent, and may be so vivid that some persons who have undergone amputation are more certain of the existence of the missing than of the remaining limb. That sensation rarely extends, however, to the whole limb. In a third of the cases of amputation through the thigh, and half the cases with amputated arms, there is a feeling that the missing foot or hand is nearer the trunk than in the corresponding intact limb. The most interesting point for the argument is that there are subjective sensations of movement in the amputated limbs. The patient is nearly always capable of voluntary change in the phantom of the missing limb, and can produce sensations of flexion and extension, if not of the whole of the joints, at least of the fingers or toes of the missing limb. Generally speaking, these voluntary efforts are injurious and produce itching at the stump; but in some cases the patient imagines complete freedom of movement in the missing hand, and says, "My hand is open, my hand is closed, now I am touching the thumb with the little finger, now my hand is in the position for writing," and so on. From these and other interesting phenomena which he describes in detail, Weir-Mitchell concludes that the will to move and the consciousness of movement are synchronous, and occur simultaneously in the centres. At each volition the consciousness of the act to be performed, with its qualities, surges up in the mind. These phenomena are erroneously attributed to impressions coming from the periphery.

(*d*) Z. Treves assumes the existence of a sense of innervation, by which we have a direct appreciation of centrifugal impulses sent out by the motor centres, because we habitually regulate the volitional impulse in such a way that the external change effected by the muscles brings about the desired effect, both in amplitude and speed, with the least expenditure of energy on the part of the muscles, independently of sensations conveyed from the periphery by the muscular sense.

A proof that this regulation of the volitional impulse really exists and is central in origin is given by the experiment of the bottle (quoted by Johannes Müller in his *Text-book*), in which if an empty bottle which the subject believes to be filled with a more or less heavy fluid is raised, it acquires unexpected velocity, and almost precedes the movement of the arm—it *flies*, in Fechner's picturesque expression. This excess of energy expended when the subject does not know if it is full or empty would not appear if the intensity of the centrifugal impulse depended solely on the peripheral sensations due to muscular activity.

In analogy with this are the phenomena described by G. E. Müller and Schumann relative to certain errors in the estimation

of weights. If a comparatively long series of tests is made with a rather heavy weight, and the experimentor suddenly has to lift a lighter weight, it will seem excessively light. If, on the contrary, the weight is made heavier, it appears much heavier than it really is. This also shows that we usually predetermine the volitional impulse, and measure it according to previous experience for the weight we are about to lift, and that these errors of judgment depend on the disproportion between the energy employed and the mass actually raised.

Treves adduces another familiar experience in support of the same point. If in coming down a staircase one step is higher or lower than the rest, we are apt to fall or stumble, because the foot is moving at a rate corresponding to the rhythm of the previous descent, and is not adapted to the unequal step.

(*e*) To prove the existence of a sense of innervation, Treves adds some ingenious remarks on the education of the volitional impulse. He points out that the less the motor impulse (which results directly from the volitional impulse) is sufficient, *i.e.* adequate to the mechanical task imposed, the greater will be the sensation of effort. The physical basis of this sensation may be numerically expressed by the reciprocal value of the product of the resistance into the square of the velocity imparted. But if the sense of effort is mainly based on the degree of tension given to the muscle, and on the time this tension lasts till the desired aim is reached, it follows that the education of the volitional impulse which serves to reduce the sense of effort to its minimum must be the result of previous experience: this cannot be explained unless we admit the sense of innervation, by which we are able to graduate the volitional impulse, and with it the motor impulse, and adapt it to the desired end. This idea of Treves agrees with Mach's proposition: that what we term *will* is no more than the sum of those states associated with the previsions of the effect that precede a movement, of which we are partially conscious. This sum must be something more than the mere mnemonic ideation or representation of movement, and something other than the sense of effort that accompanies the actual movement; both these in fact are not seldom opposed to the mechanical effects foreseen and actually obtained, as for instance in Delboeuf's experiment quoted above, in the so-called "cramps" of different professions, the ataxic movements of diabetes, and the like. The sum of the central conditions antecedent to the movement must, as Mach points out, form the content of the sense of innervation, directly perceived as such, and thus constitute the initial factor in every voluntary movement, even when by long practice it has passed into the region of the unconscious.

Mach, whose definition of a voluntary act has just been cited,

seems to admit these logical conclusions. For, in the 5th edition of his *Analysis of Sensations*, he inclines—if not directly joining with those who admit the sense of innervation—at least to leave the question open.

We must now turn to the fundamental arguments of the opponents of a sense of innervation, including the psychologists William James and Münsterberg, and the majority of living physiologists. They may be reduced to three main propositions, which we will consider in turn:—

(*a*) The first objection to the theory of a sense of innervation is derived from the clinical case recorded by Strümpell, quoted above (p. 90). In this case the motor paths are intact, because with the aid of vision the patient is perfectly able to carry out any movement at command. The paths from the hand and forearm, of both superficial and deep sensation, are, on the contrary, completely interrupted. The conditions for the so-called innervation sense are therefore intact, while those for the muscular sense are interrupted. Seeing that with his eyes shut the patient is unaware of the flexed or extended position of his fingers, is unable to maintain the position of the hand assumed when his eyes were open, or to carry out correctly the movements he is told to perform, there is here sufficient reason for denying the existence of a special central sense of innervation.

The force of this objection is undeniable. It does not, however, seem to us to cancel the weight of the above arguments in favour of a sense of innervation. We have seen that there are exceptions to the fact that amputated persons are "aware" of the lost limb, and that still more frequently they are unable to move the joints imagined in it. Strümpell's case, which deals not with an arm amputated *in toto*, but merely with interruption of the sensory paths, may count as one of these exceptions. In any case it shows that integrity of the motor paths is not enough to secure perfect execution of voluntary movements, and that we do not yet know all the internal conditions necessary to the normal functioning of the sense of innervation.

(*b*) The second objection is founded on certain experiments of Bernhardt (1872), subsequently confirmed by Goldscheider. In order to decide whether in judging of the weight of a body we employ the peripheral muscular sensations only, or a central sense of innervation as well, Bernhardt made comparative experiments and used alternately, in lifting weights, a voluntary contraction and a contraction produced by a direct electrical stimulus. In a first series of researches made on the muscles of the leg he saw that the difference between two weights is less well distinguished when the muscular contraction is produced electrically. But in a second series of experiments on the flexor muscles of the fingers he no longer found the same difference, and the judgments of the

weights raised were not perceptibly altered when the movement was excited by the electrical stimulus. From these experiments it was concluded that the supposed sense of innervation does not exist, because the muscular sense is adequate to subserve the estimation of the differences in weight.

On closer investigation, however, these experiments, which otherwise gave no constant results, only show that in judging weights the sense of effort, due to the resistance which the muscles encounter in lifting the weight, is more important than that of the central innervation sense, which we are compelled to admit on other irrefutable grounds.

(*c*) The third objection to the sense of innervation is drawn from the fact that independently of sensations of peripheral origin we are not able to prove any direct and unmistakable central sensations of innervation. Ferrier more particularly uses this argument in opposing the theories of Bain and Wundt:—

"If the reader will extend his right arm and hold his forefinger in the position required for pulling the trigger of a pistol, he may without actually moving his finger, but by simply making believe, experience a consciousness of energy put forth. Here, then, is a clear case of consciousness of energy without actual contraction of the muscles either of the one hand or the other, and without any perceptible bodily strain. If the reader will again perform the experiment, and pay careful attention to the condition of his respiration, he will observe that his consciousness of effort coincides with a fixation of the muscles of his chest, and that in proportion to the amount of energy he feels he is putting forth, he is keeping his glottis closed and actively contracting his respiratory muscles. . . . In the contraction of the respiratory muscles there are the necessary conditions of centripetal impressions, and these are capable of originating the general sense of effort."[1]

This objection is easy to meet. If the feeling of innervation is to coincide with the motor impulse, that is with the centrifugal wave of excitation sent out along the motor paths, it must obviously be absent when we imagine that we send it out, but do not really do so. The whole of Ferrier's reasoning merely shows that the sense of innervation cannot function unless there is a simultaneous muscular contraction, so that it is impossible to separate the sensations of central from those of peripheral origin. But this does not refute the theory of a sense of innervation if other powerful arguments speak in its favour.

On the other hand, it may legitimately be maintained that the central sensations of innervation, particularly in habitual movements, normally lie beneath the threshold of consciousness. The same may be said of the sensations of peripheral origin that

[1] Ferrier, *The Functions of the Brain*, 1876, p. 223.

accompany the movement. In our habitual movements we are not aware of overcoming resistance, so long as it is confined to the weight of our limbs. But this does not prevent us from regulating the impulses in voluntary acts, so that they perfectly fulfil their purpose. In regard to the innervation of the eye-muscles Mach remarks: "Thanks to the organic arrangement and long practice we straightway employ the innervation necessary to fixate any object, of which the image falls upon our retina. Innervation is only disturbed when the external motor forces are not associated with the voluntarily measured innervation."

It is a matter of common knowledge that the sensations originally present in our acts become less and less vivid with practice, till at last, as they pass into the region of the unconscious, they become mechanical — or *automatic*, as they are usually termed (an ambiguous and unfortunate expression). So that the absence of any clearly perceived sensation of the act of innervation is not sufficient to justify the statement that it was not originally more or less conscious. Such are the delicate mechanical movements by which the artist performs a musical piece on different instruments, as contrasted with the long and tedious practice required before the piano or violin can be mastered.

Again, while it is fully proved that the motor disturbances in ataxy produced by disease of the dorsal roots are due exclusively to the diminution or loss of the muscular sense, it would be a bold assertion to declare that all cases of disturbance of voluntary motility can be explained without the assumption of the innervation sense. This would lead, as Treves pointed out, to the conclusion that we can never foresee the external consequences of our voluntary acts, and never avail ourselves of the most favourable conditions, in order to reduce the sense of effort to its lowest degree. G. E. Müller and Schumann—who deny the sense of innervation—speak of a voluntary adaptation to resistance which they attribute to the tendency of motor and sensory activities of certain intensities and rhythm to become automatic by habit. This differs little, as Treves rightly points out, from the idea of an education of the impulse and accompanying conscious and primitive gradation of innervation, which these authors expressly denied.

The logical conclusion from the whole of this discussion is that voluntary acts are normally regulated by sensations of peripheral origin, which we have considered under the head of *muscular sensations*, and by those of central origin, which are known as *innervation sensations*.

VIII. In the last chapter when discussing tactile or pressure sensibility we were unable to bring out its full importance from the psychological point of view, because the perceptions and ideas

with which it is connected are nearly always intimately connected with the central and peripheral sensations that coincide with voluntary acts. In the same way the preceding remarks on the muscular and innervation senses do not sufficiently emphasise their psychological importance, because in analysing our perceptions of movement we cannot separate them from the tactile sensations with which they are nearly always accompanied in life.

Bernstein rightly distinguishes between *passive* and *active* tactile sensibility: the former comes into play when a body is brought into contact with, or exerts pressure on, the immobile cutaneous surface, *e.g.* on applying the two points of Weber's compasses to the skin; the latter when we pass the hand or fingers to and fro over the surface of a body, and move or lift it, so as to discern its form, size, resistance, weight, and other accessory physical characters. This last is the usual application of the tactile sense; but it is plain that in using active touch, and in touching objects, the tactile sensations must be combined with muscular sensations or the sense of movement. Now that we have analysed these sensations separately it will be well to put them together and compare them, the better to understand their nature and relative physiological and psychological importance.

We have seen that we possess the capacity of localising tactile sensations more or less precisely at different points of the skin, according to the relative number of the touch spots and the higher or lower threshold of excitability in the different regions. Muscular sensations, on the contrary, are very vaguely localised. Generally speaking, we do not feel the contraction of the muscles, which are the active organs of movement, but only the movement or displacement of the limb. It is only on focussing our attention sharply that we succeed in vaguely localising sensation in the joint, or the muscle or group of muscles, that is contracting. Normally we localise the muscular sensation according to the signals received at the same time through the senses of touch and vision; and when these are excluded we localise the motor sensations according to the mnemonic signs which we possess of the visual and tactile sensations by which they are usually accompanied. If, for instance, with the eyes closed we trace figures in the air with the extended forefinger, we are as plainly aware of the tracings described by the end of the finger as if we saw them with our eyes, while in reality the surface of the fingertip receives no impression. The physiological basis of this percept is certainly formed by the central impulses and simultaneous muscular contractions of the limb which displace the joints in various ways, and must vary with the variation of the angles, straight lines, or curves that we trace in the air with the

finger-tip. Why then do we not perceive the figures traced by the finger in our joints and muscles, but in a different and far-off spot which is not the seat of any excitation? Evidently because from long habit we explore the objects which surround us with our eyes and fingers, so that the memory of the things felt on the skin and the extent of the space seen are necessarily revived each time the contraction of the muscles moves the articulations of a limb, even when we do not see them move, and when the sense of touch is hardly, if at all, excited.

This observation is of great importance, because it proves incontestably that the so-called "muscular sensations," which as we have seen are principally due to the sensibility of the joints, are in themselves only forms of the *common sensibility* with which all the internal organs supplied with afferent nerves are provided. Accordingly, we are unable to objectify the muscular sensations or transform them into perceptions, without the collaboration, direct or indirect, actual or mnemonic, of tactile and visual sensations. And those authors are wrong who hold the muscular sense to be a special sense, like the tactile sense, the visual sense, and so on.

Just as the tactile sense is complementary to the muscle sense, so we may say that muscular sensations reinforce tactile sensations and contribute in developing their capacity of localisation.

As Weber pointed out, we may reasonably hold that all our sensations, including the cutaneous, are at first devoid of the power of localisation. They represent simple states of consciousness, differing in quality and intensity, but giving no notion of place, and having no local sign. On the strength of certain researches of Preyer on the chick embryo, it may be asserted that in the ontogenetic development of the senses common sensibility in the obscure form of internal bodily sensation appears first; cutaneous sensibility only begins to appear at the tenth day of incubation. Before that it is possible to apply every kind of mechanical, chemical, and electrical stimulus to the skin without evoking the slightest reflex movement; but at the end of the fifth day the embryo exhibits automatic movements due to internal excitations. The same facts were noticed in the mammalia embryo also. So that of foetuses in general, including the human, it may be admitted that obscure muscular sensations precede those of the special senses. This is highly important from the psychological point of view.

How does the capacity of tactile and cutaneous localisation develop in the new-born animal? We may legitimately assume that its development is promoted by the activity of the muscles and the resulting muscular sensations. If Weber's tables for the delicacy of tactile sensibility are consulted, it will be found that he gives first place as surfaces of extreme sensibility to the tip of

the tongue, the red edges of the lips, and the ends of the fingers (see p. 42). This dominant development of tactility in the tongue and lips is satisfactorily explained—if we admit that the muscular sensations reinforce the power of cutaneous localisation—by the fact that amongst the earliest, most important, and most eager movements of the new-born is that of sucking, which is evoked by an instinctive, central impulse, and is accompanied and regulated by the sensations derived from the activity of the lingual and labial muscles. The great delicacy of tactile sensibility in the finger-tips and palms of the hand, again, is due to the fact that it is by exercising the active touch of the hand, accompanied by various movements of the limbs, that the infant seeks and finds the breast of its nurse, that the growing child gathers its first experiences from its own body or from external objects, that the adult, lastly, accomplishes the many actions that enable him to carry on different manual trades.

The development of muscle sensibility and the corresponding improvement in cutaneous localisation take place very slowly in children, judging from the difficulty with which they learn to touch objects, direct their hands to a given spot, make their first steps, and so on.

In adults, according to Goldscheider's data, the muscular sense reaches a high degree of delicacy owing to the sensibility of the joints. And yet when a person with closed eyes is made to imitate with one arm movements that have previously been carried out with the other, the range of the movement being the same but its direction altered, or when the conditions of experiment are otherwise changed, there are marked discrepancies between the movement the subject believes himself to be making and that really carried out. This does not agree with the delicacy of discrimination between active and passive movements described by Goldscheider.

Other experiments of Beaunis and Stanley Hall demonstrate the normal imperfection of the muscular sense when it acts alone in controlling the direction, range, and rate of a movement. Two symmetrical movements carried out with the two upper limbs, with every intention of making them equal, invariably show a preponderance to right or left according to the idiosyncrasy of the subject, quite apart from right- or left-handedness.

When a thread carrying a weight is supported by the finger, there is a sensation of something external to the finger which offers resistance, but this is obviously not an elementary sensation but a resultant of various factors. The discrimination of different weights was proved by Hering to rest on the comparison of different elementary sensations of tension, position, excursion, and rate of movement in addition to tactile sensibility. This is why weights are better appreciated when they are raised than when

they rest upon the motionless hand, as Weber first pointed out. Our judgments are based less on tactile sensations than on the complex kinaesthetic sensations by which muscular acts are accompanied.

According to Merkel's experiments, when weights of between 200 and 2000 grms. are estimated by counter-pressure on the scale-pan of a balance, the liminal sensibility is about $\frac{1}{13}$th of the whole weight if the finger remains at rest, while if the scale-pan is compressed by voluntary movements it is about $\frac{1}{19}$th. The data collected from various authors (Weber, Fechner, Jacoby, Goldscheider and Blecher, Langlois and Richet), however, differ too much for any positive value to attach to this experiment.

According to G. E. Müller and Schumann, in raising two weights for purposes of comparison we generally employ the same motor impulse for both weights, and our judgment is based essentially upon the different rate at which they move, since from previous experience we estimate the one that moves faster as the lighter.

According to Jacoby, the latent time of a movement is an important factor in judging of weight. For a given weight a given lost time corresponds with a certain intensity of innervation effort, and if the effort remains constant the latent period is proportional to the value of the weight. Another factor in the discrimination of weights, according to Jacoby, is the facility with which the movement can be stopped, which varies according to the weight raised.

The analysis of the factors in the judgment of weights made by Z. Treves in his ergographic studies led him, on the other hand, to hold that the object of the judgment is not so much the weight in itself as the intensity of the effort, which is essentially due to two factors, viz. the average muscular tension and its duration. This element of judgment, however, is strictly dependent on the central impulse of innervation, and varies indirectly to the latter. So that the enormous variations and errors that generally occur in this class of observations must be interpreted as the indirect expression of the fluctuations of the motor impulse, which is the expression of a neural act akin in its nature to attention, and is highly unstable and insusceptible to direct control. With the same weight the physical factors on which our judgment is based may vary considerably with the variation of the impulse. And the impulse, like all voluntary acts, fluctuates widely, even when it is directed to a given end, with known conditions of resistance. Treves proved this directly by showing that these oscillations of impulse occur also in rhythmical movements with a maximal voluntary impulse, and may, particularly in long-protracted work, have the effect of reducing the effort so much as to mask the progressive muscular deterioration.

The above discussion is necessary to give the student some idea of the different sensory factors of central or peripheral origin, which necessarily enter into the formation of the so-called active tactile perceptions (in which the cutaneous sensations are associated with a preponderance of various kinaesthetic elements) and of the different values ascribed by the physiologists who have studied this difficult subject to the various factors concerned in the discrimination of weights.

IX. In Chapter VII. of the last volume we discussed the Hind-brain at length as the seat of the organs of subconscious sensations, on which the normal tone of the muscles largely depends. We saw that these subconscious sensations are maintained by a number of afferent paths which are in direct or indirect relation with the cerebellum and spinal bulb. Of these afferent paths we emphasised the importance of those represented by the vestibular roots of the eighth cerebral nerves, by which

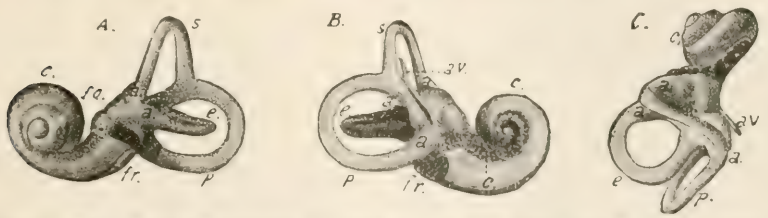


FIG. 44.—Model of the left labyrinth of human ear; *A*, from outer side; *B*, from inner side; *C*, from above. $\frac{2}{3}$. (Henle.) *s.*, superior; *p.*, posterior; *e.*, external (lateral), semicircular canal; *a.*, ampullae; *a.v.*, aqueduct of vestibule; *f.o.*, fenestra ovalis (vestibuli); *f.r.*, fenestra rotunda (cochleae); *c.*, coiled tube of cochlea.

the so-called non-acoustic labyrinth is innervated (Vol. III. p. 461). At this point we may discuss the many experimental facts that have been collected with reference to this most delicate peripheral sense-organ, and the various theories put forward for their interpretation. A full account would, however, exceed the limits of this text-book, and we must confine ourselves to discussing the most important to our own point of view.

We must begin with a brief description of the anatomy of the Internal Ear or Labyrinth, referring the reader for greater detail to anatomical text-books.

The internal ear is morphologically divided into two parts—the Cochlea, innervated by the ramus cochlearis, and the Vestibulum, consisting of the three semicircular canals, the utricle and the saccule, innervated by the vestibular branch of the eighth nerve. Physiologically, too, this division seems to be justified. (See Vol. III. p. 405.)

The cochlea is a later formation than the vestibular organs. In fishes it is quite rudimentary, and is represented merely by the *lagena*, which is a small appendage of the saccule. In

amphibia it is much more developed, and in reptiles it develops

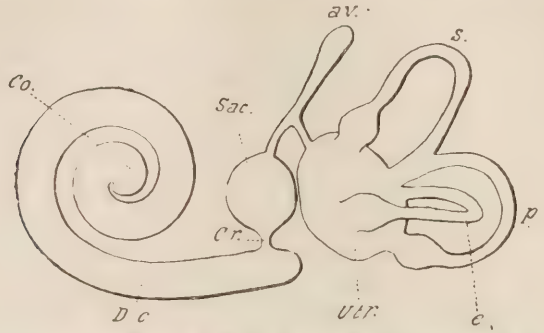


FIG. 45.—Membranous labyrinth of left side seen from without. (Merkel.) *Co.*, cochlea; *D.c.*, ductus cochlearis; *Sac.*, saccule; *Utr.*, utricle; *s.*, superior; *e.*, external (or lateral); *p.*, posterior semicircular canal; *a.v.*, aqueduct of vestibule; *Cr.*, canalis reuniens.

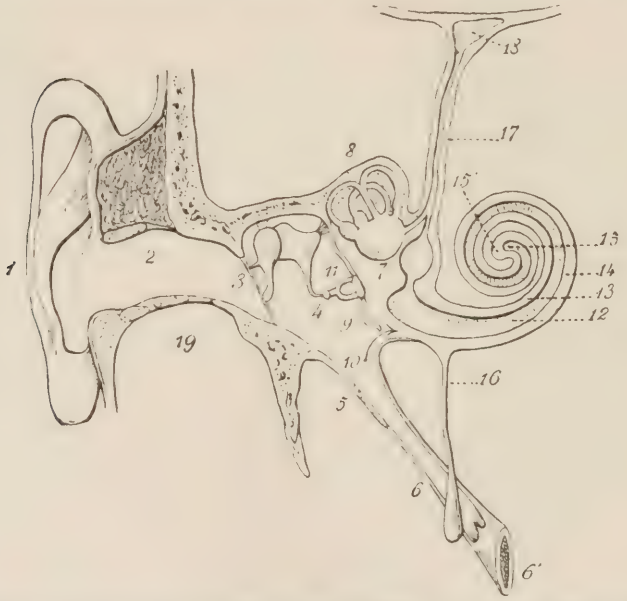


FIG. 46.—Diagram of entire human auditory organ. (Debierre.) 1, auricular lobe; 2, external auditory meatus; 3, tympanic membrane; 4, stapes attached to base of fenestra vestibuli; 5, bony part of Eustachian tube; 6, its cartilaginous parts; 6', mouth of tube; 7, vestibular cavity filled with perilymph; 8, semicircular canals and utricle; 9, promontory; 10, fenestra cochleae (the arrow indicates the tympanic opening of the cochlea); 11, tympanic cavity filled with air; 12, cochlear duct filled with endolymph, united to saccule of vestibule by a narrow junction canal; 13, scala vestibuli; 14, scala tympani terminating in fenestra cochleae; 15, apex of cochlear canal, where the two walls unite at 15'; 16, cochlear aqueduct; 17, vestibular aqueduct; 18, endolymphatic sac; 19, parotid region.

progressively from the chelonians and ophidians to the saurians and crocodiles. It is only in these last and in birds that the

cochlea gradually acquires a spiral arrangement. Finally in mammals it reaches its greatest development in the form of a long twisted tube, with one and a half to four or more spiral turns. The cochlea, with the nervus cochlearis which forms a delicate end-organ within it, undoubtedly represents the organ of hearing, as will be fully discussed below.

The membranous labyrinth with the terminations of the vestibular branch of the eighth nerve forms another delicate sense-organ which phylogenetically represents the first stage in the differentiation and perfecting of primitive cutaneous sensibility. It is contained within the bony labyrinth hollowed out of the petrous bone, the form of which is clearly seen from the models obtained on pouring molten metal into the cavity of the labyrinth (Fig. 44). The formation of the membranous labyrinth and its different parts is shown in Fig. 45. The membranous labyrinth filled with endolymph is contained in the cavity of the vestibule, which in its turn is filled with perilymph. Fig. 46 gives some idea of the topographical relations of the labyrinth with the tympanic cavity and the external ear.

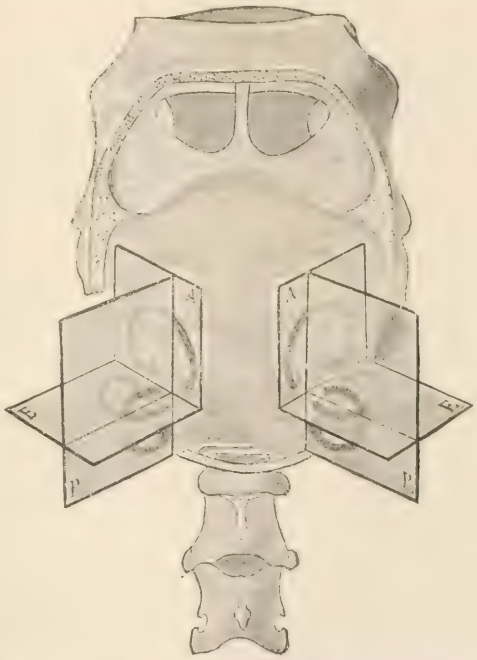


FIG. 47.—Diagram of orientation of semicircular canals in pigeon seen from behind and within after opening the skull. (Ewald.) The anterior canal lies in plane *A*; the external canal in plane *E*; the posterior canal in plane *P*.

The semicircular canals are orientated according to the three planes of spatial dimension. On each side there is an external canal, an anterior canal, and a posterior canal. As appears plainly in Fig. 47, the two outer canals lie almost exactly in the same horizontal plane; the planes of one posterior canal and the anterior canal of the opposite side are almost exactly parallel, and form with the median plane an angle of about 45°. The six semicircular canals thus form together three planes, one horizontal and two vertical, which are perpendicular to each other and to the horizontal plane, so that they are orientated

almost exactly along the three dimensions of space. The two vertical canals on each side unite together in their posterior part, so that in the utricle there are five instead of six openings to the canals, as shown in Fig. 45.

Each canal is dilated at one end into a swelling or ampulla, in which a branch of the vestibular nerve ends in the crista acustica, which rises almost to the axis of the canal, and is clothed with special sensory cylindrical cells. These cells of the sensory

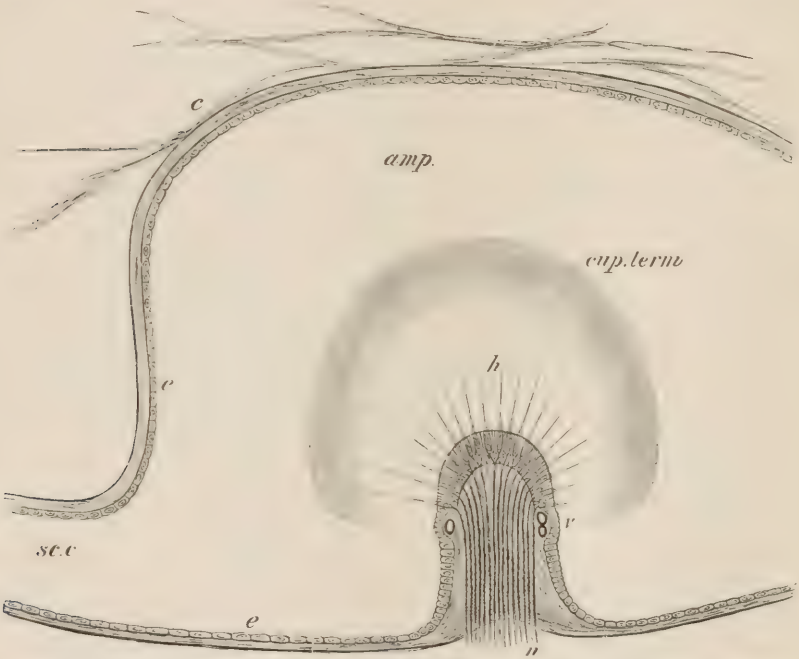


FIG. 48.—Longitudinal section of ampulla of a fish, taken through the crista acustica. Diagrammatic. (E. A. Schäfer.) *amp.*, cavity of the ampulla; *sc.c.*, semicircular canal opening out of it; *c.*, connective tissue attached to wall of the membranous ampulla and traversing the perilymph; *e.*, *e.*, flattened epithelium of ampulla; *h.*, auditory hairs projecting from columnar cells of auditory epithelium into the cupola, *cup. term.*; *v.*, limit of the auditory epithelium on the crista; *n.*, nerve-fibres entering base of crista, and passing into the columnar cells.

epithelium carry long flexible hairs, which are thicker than those of ordinary ciliated epithelium, and are held together by a mucous, gelatinous mass so that they are unable to move freely in the endolymph (Fig. 48).

The nerve end-organs of the utricle and saccule are very similar to those of the ampullae. These special sense-organs, known as the macula acustica, are formed by the endings of twigs of the vestibular nerve (Fig. 49). The remainder of the wall of both utricle and saccule is destitute of nerves.

The sensory epithelium of the macula has shorter hairs than

those of the crista. These hairs are also held together by a denser mass (*otoconium*) and contain a small amount of carbonate of lime (*otoliths*) (Fig. 50). All vertebrates except mammals have three otolithic organs on each side (*maculae utriculi, sacculi, et lagenae*); mammals have only two, because they have no lagena, which has become transformed into the cochlea.

The earliest view of the different functions of the two prin-

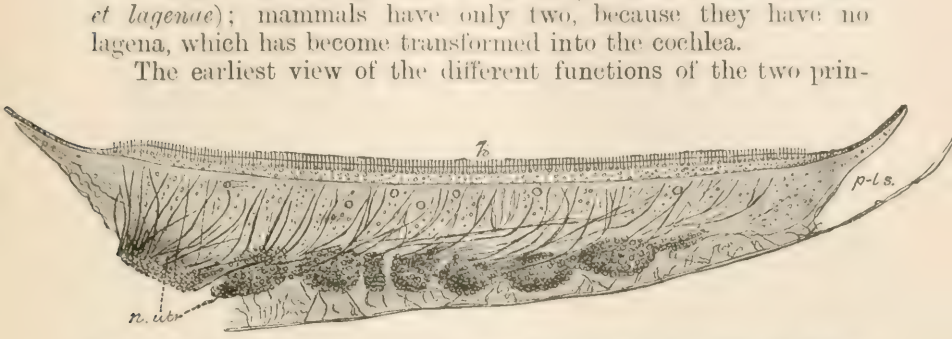


FIG. 49.—Section of the macula acustica of recessus utriculi, human. Magnified. (G. Retzius.) *n.utr.*, bundles of utricular branch of the eighth nerve; *h.*, hair-cells; *p-l.s.*, perilymphatic space.

cipal divisions of the membranous labyrinth is that of Scarpa (1772), who attributed to the ampulla and utricle the capacity of conducting sound-waves from the bones of the skull, whereas they are conducted by the tympanic cavity to the cochlea. This theory rests exclusively on the anatomical fact that the vestibular labyrinth is in closer relation with the bones of the skull, while the cochlear labyrinth is in more direct connection with a special apparatus for conducting sounds by the air.



FIG. 50.—Otoliths. (Schwalbe.)

Dugés (1838) propounded the far more satisfactory hypothesis that the saccules of the vestibule are excited by noises, that is by irregular sound-waves, and measure the intensity of these, and thus estimate their distance, while the neural apparatus of the cochlea is capable of excitation by musical tones. Helmholtz supported this theory without adducing any conclusive proof of it. It was founded on a phylogenetic concept which led to the assumption that the cochlea, the best developed organ, was intended to convey the finer and more complicated auditory sensations in the higher vertebrates, while the saccules, which form the whole labyrinth in the lower vertebrates, are only able to receive coarser auditory sensations, and at most the simplest musical tones.

If auditory sensations were common to all classes of animals provided with otocysts, this theory would be impeccable in a general sense. More recent observations, however (Vol. III. p.

406), have shown that fishes are destitute of auditory sensations (Bateson, Kreidl, Lee). According to the latest observations of Parker and of Zenneck, some fresh-water fishes (*Leuciscus*, *Alburnus*) are exceptions to this rule, because under certain conditions they react to sound-vibrations. But it has not been and cannot be shown that in these animals such reactions are preceded by acoustic sensations, and not merely by sensations of vibration. On the other hand, the fact that in the higher vertebrates the destruction of the cochlea alone is sufficient to produce total deafness shows that the vestibular organs are not able to subserve any sensation of noise or sound. Nor is it probable, as Breuer points out, that the maculae and crista are organs of acoustic sensation, because the hairs of the sensory epithelia are bound together by mucous matter which impedes their free vibration.

This excludes another early view put forward by Autenrieth (1801), Kerner, and Duget, who supposed that the semicircular canals subserved perception of the direction of sounds. This hypothesis was upheld later by Lussana, particularly from the syndrome of Menière's disease, which will be discussed below.

The founder of the modern theory of the functions of the non-acoustic labyrinth was Flourens (1828), who found that after lesions or excitation of the semicircular canals in pigeons and mammals characteristic forced movements were obtained. After section or removal of one semicircular canal he noted pendular or nystagmic movements of the head, the direction of which depended on the plane of the canal destroyed or removed (the horizontal plane if the external canal were injured, one of the two vertical planes if the upper or lower canal suffered). These phenomena diminish and pass away after a certain time. But if the canals of the opposite side are destroyed or removed, the pendular movements reappear with greater intensity. They return spasmodically whenever the animal is in any way disturbed. The nystagmus of the head is associated with nystagmus of the eyes, often with a tendency to fall or roll over, with vomiting, tachypnoea, tachycardia, etc. The operated pigeon can no longer fly and has difficulty in feeding itself and in walking. The greater the injury to the vestibular organs, the more intense and persistent are the motor disorders. But if the cochlea is spared there will be no appreciable alteration of hearing, while if the cochlea is removed without injuring the canals, deafness results in rabbits without abnormal movements.

Flourens first showed experimentally that the vestibular organs are of no importance to hearing, while they are of supreme significance in the complex movements of animals. The motor phenomena which he described were universally confirmed, but

they received different interpretations, according as the disorders were held to be phenomena of irritation or of deficiency.

In continuance of Flourens' experiments Goltz (1870) described certain motor disorders consequent on lesions of the labyrinth, not only in mammals and birds, which exhibit nystagmus of the head and eyes as described by Flourens, but also in frogs and fishes, which do not present these phenomena, and in invertebrates after removal of the otoliths. The disorders described by Goltz consisted in forced positions taken up by the animals after operation, and uncertain equilibrium in locomotion. The forced positions are specially apparent in fishes, frogs, and in aquatic invertebrates, operated on upon one side only. The uncertainty of locomotion, on the contrary, is more apparent in mammals and birds after bilateral operation. These phenomena bear a strong resemblance to those that result from uni- or bilateral extirpation of the cerebellum, which we have already discussed.

As shown in Vol. III. p. 463, the phenomena studied by Goltz led him to consider the non-acoustic labyrinth as the seat of the sense of position for the head, on which depends the function of equilibration. The disorders consequent on the lesions of the canal depend, according to Goltz, on the absence or perversion of sensations of the position of the head. He assumes that each ampulla is excited by the gravity of the endolymph contained in the corresponding canal; so that with each active and passive movement of the head, there must, as the canals change their position, be a change of pressure in the endolymph, sufficient to excite one or other of the ampullae.

Numerous objections were made to this theory. We must here confine ourselves to stating that the disorders of locomotion described by Goltz do not last long; that there is a stage at which they have not yet disappeared, although the animal's sense of the position of the head is perfect; that, lastly, the canals may be emptied of all their endolymph, without producing any disorders of equilibration.

In his early work (1873) v. Cyon, starting from Goltz' theory that the semicircular canals are organs whose office it is to give the sensations of the position of the head, held that these sensations are necessary in order to acquire the idea of a tri-dimensional space. He repeated the experiments which Breuer had made a few months before (1872) on the effects of the gravity of the endolymph, as assumed by Goltz, of opening the bony canals, of aspiration of the perilymph with filter paper, and of compression of the membranous canal by tampons, etc., with the same results as Breuer. Cyon therefore excludes the stimulating action of the gravity of the endolymph, but determined no other physiological stimulus for the canals. He only vaguely states that the canals may be excited by the oscillations of the otoliths and endolymph,

whether these are or are not due to sound-waves. But the otoliths lie in the saccules of the vestibule, not in the canals, and if it be admitted that these oscillations and those of the endolymph can stimulate the canals, or that these oscillations are in relation with the position of the head, then Cyon's theory merges into that of Goltz; or if this be not admitted, then we cannot see how these oscillations can give information as to the position of the head.

From the physiological standpoint the *spatial sense* of Cyon and the *sense of equilibrium* of Goltz are analogous in significance.

Nevertheless it was Cyon who demonstrated the effect of artificial stimulation of the canals upon the movements of the eyes. Flourens, too, noted movements of the eyeball after section of the canals in rabbits, but, according to his observations, these movements ceased when the head became fixed, and must therefore be regarded as compensatory acts, associated with the head movements. Cyon, on the contrary, showed that the nystagmus of the eyes in rabbits did not cease when the head became stationary, but increased; and further showed that strabismus and nystagmus were produced in rabbits by direct stimulation of the canals with the induced current, and, like the movements of the head, occur in different directions, according to the canal stimulated.

Neither we ourselves nor Stefani, who is a competent judge, have been able to see the physiological importance of Cyon's later experiments. His conclusions from dancing mice have, moreover, not been confirmed by other experimenters.

The theory of Goltz was taken up and defended in different forms by a number of other authors. Purkinje (1820) had shown, in his studies on vertigo, that passive rotation of the whole body round its long axis produced a definite sensation (independent of the visual sensations) of rotatory movements in different directions, according to the plane of rotation and the position of the head. He also produced the same sensation by passing a constant current through the head. Purkinje supposed that the rotatory vertigo and galvanic vertigo were produced through the cerebellum, and were excited by the movements of the circulating fluids caused by rotation, and by the anaemia and hyperaemia produced by the galvanic current.

After Goltz published his theory Breuer (1875–76), and almost simultaneously Mach and Crum Brown, repeated the old experiments of Purkinje with a view to finding a more adequate interpretation of the phenomena described by Flourens and Goltz.

Mach found that if the subject of experiment is seated on a stool fixed to a platform that can be rotated round a vertical axis at a known distance from the axis, and is turned round with his eyes blinded and his head in the normal position, he is distinctly aware of the rotation in the horizontal direction to right

or left, so long as the angular velocity is increasing. When the velocity becomes uniform this sensation gradually disappears. When the speed diminishes the subject has an illusory sensation of rotating in the opposite direction. This illusory sensation reaches its maximum intensity when the rotation ceases, lasts for a few seconds after it has stopped, and disappears directly the movement recommences. If the bandage is taken off the eyes during the sensations of vertigo, visual vertigo will be substituted for the subjective sensation of rotation, so that all the objects in the environment seem to turn in the same direction. This post-motor visual vertigo is due to nystagmus of the eyes, as Purkinje recognised.

If the rotatory movements are made with the head inclined sideways, upward, or downwards, there will be a sensation of turning, not on a horizontal plane, but on a plane vertical to the axis of the head. If, during rotation of uniform velocity, when all sense of movement is lacking, the head moves from the vertical to an inclined position, the sense of rotation reappears, but in the inclined plane that corresponds to the degree and direction of the inclination of the head. These phenomena prove that the organs by means of which the rotatory movements are perceived lie in the head.

In addition to these phenomena, there is seen during the acceleration of the rotatory movements not only in man, but also in mammals and birds—blind or blindfolded—nystagmus of the head and eyes in the direction opposite to the movement, which becomes less and ceases as the angular velocity becomes uniform. When the rotatory movement is slowed down and stops, the nystagmus of the head and eyes reappears, but in the direction of the plane of rotation, lasting for some seconds and accompanied by oppression in the head, vertigo, tendency to vomiting, etc. These effects, as Breuer showed, are very similar to those above described after section or removal of the semicircular canals.

To understand this fact it is necessary with Breuer, Mach, and Crum Brown to admit that there is in the head a sense-organ that is excited by its rotatory movements in various planes, and the only organs that can reasonably be credited with this office are the semicircular canals, owing to their arrangement in three planes vertical to each other.

This theory finds confirmation in the observations of James, Kreidl, and Bruck on deaf-mutes. According to these observations, in deaf-mutes (in a proportion corresponding to that in which the semicircular canals are so much altered that it is impossible that they should function) arrest of passive rotation with the eyes bound does not produce rotatory vertigo, and nystagmus of the eyes and head is absent at the commencement of rotation.

Another experiment performed by Breuer on pigeons deprived of the labyrinth showed that in these animals there is no rotatory vertigo when they are blindfold or blinded. This fact was at first disputed by Cyon and Hermann, but was ultimately confirmed by Ewald, and by Strehl, a pupil of Hermann.

Purkinje's experiments on pure galvanic vertigo were repeated and better elucidated by Hitzig. He showed that during the passage of a constant current of a given intensity, applied over the two mastoid regions, there is, when the eyes are closed, a sensation of falling to the side of the kathode, while first the head and afterwards the body are bent to the side of the anode, as if to avert a fall. If the eyes are kept open during the passage of the current the environment seems to turn towards the kathode, owing to the involuntary nystagmus of the eyes which occurs if the current is tolerably strong.

Breuer observed approximately the same phenomena in normal pigeons, and found they were no longer produced when the labyrinth was destroyed: this was confirmed by Ewald, but disputed by others. The labyrinthine origin of galvanic vertigo was confirmed by Pollak in deaf-mutes. He found that in deaf-mutes, in whom rotatory vertigo was absent, galvanic vertigo was also absent.

Independently of the passive movements of the organism as a whole, we are aware, even with our eyes shut, of the position of our body in the environment, if not in relation to the four points of the compass, at least to the vertical, that is, to the direction of gravity. It seems clear that this perception of the vertical depends on tactile sensibility. In fact, the surfaces of support on which the body rests in the erect, seated, or recumbent posture are subjected to pressure or deformation by the weight of the body, and this gives rise to tactile perceptions on which the power of orientating our body along the line of gravity depends. But that other than tactile sensations are involved may be deduced from the fact that when we are immersed under water, although we lose these tactile sensations, we are still able to orientate ourselves relative to the vertical. Accordingly we must conclude that we possess a sense-organ which makes us aware of the direction of the force of gravity, apart from sight and touch. Many facts lead to the conclusion that the labyrinth is the sense-organ in question. But we need only refer to the conclusions of James, who saw that if deaf-mutes, who have no rotatory vertigo, close their eyes under water, they are no longer aware of their position in relation to the vertical, and are seized with vertigo.

The ingenious hydro-mechanical theory propounded by Mach and adopted as a whole by Crum Brown and Breuer may be set out in a few words. It purports to explain how passive and active movements and static postures are capable of exciting the

nerve-endings of the ampullae and maculae of the labyrinthine saccules, and of producing the sensory and motor phenomena we have been discussing.

According to Mach, both in rectilinear and in angular and rotatory movements, the endolymph presses on the wall opposite to the direction of the movement. At each variation in the rate of the movement there is a variation in the pressure, and a consequent variation in the stimulation of the ampullary cristae in the plane of which the movement takes place.

The motor reactions produced by experimental labyrinthine sensations are reflex phenomena of a compensatory character, which tend to compensate the real or illusory effects of rotation or rectilinear displacement.

In the static position, according to Breuer, it is not the cristae but the maculae of the saccules that are excited by the gravity of the otolith. As the otoliths have a higher specific gravity than the endolymph in which they are bathed, the hairs of the sensory cells must be pulled in a different direction from that of the position of the head; this produces the excitations which give rise to the sensation of this position in respect of the line of gravity, and the reflex movements of the eye that are co-ordinated with it.

According, therefore, to the theory of Breuer, Mach, and Crum Brown, the labyrinth is composed of three distinct sense-organs: the cochlea with the organ of Corti, for which the adequate physiological stimulus consists in sound-vibrations: the canals with the cristae acusticae, which are physiologically stimulated by the movements of the head: the vestibular saccules with the maculae, the stimulus of which is the movement of the otoliths, and particularly the variations in the rate of the rectilinear movements, both on the horizontal and on the vertical planes. The cochlea is the organ of hearing, as we shall see below; the canals are the organs on which depend the experimentally produced sensations of rotatory and galvanic vertigo, and which normally influence the complicated function of equilibration by means of obscure sensations: the saccules are the organs on which the subconscious sensations that we normally have of the direction of the line of gravity, and thus of the position of our body in relation to the environment, depend.

This ingenious theory accounts for nearly all the phenomena described in the various experimental researches carried out on the labyrinth of vertebrates from Flourens to Goltz, Goltz to Breuer, Mach, and Crum Brown. But before we accept it unconditionally it is necessary to refer to another important series of experiments on the labyrinth that have added greatly to our knowledge of this important sense-organ, and enlarged the conception of their functional significance.

Ewald (1887–89, 1892–6) undertook an experimental study of

the whole of the phenomena consequent on partial or total uni- or bilateral lesion in the end-organ of the eighth nerve, and by his ingenious methods brought to light certain facts that had escaped his predecessors, including his own master, Goltz. These are the more remote residual effects of labyrinthine deficiency and consist in the abnormal relaxation of inactive muscles (muscular atony), the diminished energy displayed during activity (asthenia), and the defective precision of the movements which they execute (astasia). Ewald also claims that muscular sensibility is diminished in the dog that has lost its labyrinth, but this is less a fact than an interpretation of the observation that the animal draws back its paw more slowly if the support beneath it is taken away, which may be due to the atonia and asthenia of the muscles.

There is accordingly no sharp line of demarcation between the phenomena described by Goltz and those observed by Ewald: both have the same origin. Moreover, it is clear that removal of the labyrinth on one or both sides produces effects that are approximately identical with those we have already described at length, after removal of half or the whole cerebellum. The duration of the effects of lesions of the labyrinth is, however, less than those of cerebellar ablation. According to Ewald, the disturbances due to the destruction of one labyrinth disappear after a week, of both after about a month.

In Chapter VIII. of the last volume it was shown, particularly from the work of Stefani and Deganello, that the twigs of the vestibular nerve, which innervate the cristae of the ampullae and the maculae of the vestibular saccules, are in close anatomical relation with the hind-brain, *i.e.* with the cerebellum and bulb, and that the experimental facts set out by Ewald, Stefani, and Deganello as a whole support the conclusion that these parts of the brain represent the most immediate centres of the vestibular division of the eighth nerve. Our task is therefore only to bring into relation with the functions of the cerebellum the most probable theories that have been propounded in regard to the functions of the vestibular organs.

Ewald, in agreement with Breuer, Mach, and Crum Brown, assumes that the labyrinth can be excited mechanically by active and passive movements, rectilinear or angular; but in order to explain the atonic, asthenic, and astatic effects which he has shown with so much operative skill, he further assumes that the nerve-organs of the labyrinth are in tonic excitation during the waking state, which reflexly determines the tone of the striated muscles, on which their normal functions depend.

Ewald's theory of labyrinthine tone harmonises perfectly with our own theory of cerebellar tone. It explains the certainty of equilibrium of the body in standing and walking, the promptness with which equilibrium is regained by compensatory movements

when it has been lost, the general muscular atony that accompanies vertigo; it also explains the effects described by Goltz and Flourens after lesions of the semicircular canals.

It would, however, be a mistake to assume that labyrinthine tone is an indispensable condition to the normal functions of the muscles. For we have seen that in deaf-mutes, who exhibit no rotatory or galvanic vertigo, the muscles function regularly in the movements of the limbs, in standing, and in walking. On the other hand, we have noted that the motor disorders produced by destruction of the labyrinth or section of the eighth nerve in animals disappear, or become perfectly compensated, in a comparatively short time. It is thus evident that the labyrinth does not contain the only afferent nerve paths that reflexly keep up the tone of the muscles. The far longer duration of the effects of cerebellar as compared with those of labyrinthine deficiency shows that cerebellar tone is maintained by other than the vestibular paths; many other afferent cerebellar paths ascend in the cerebro-spinal axis, particularly those coming from the joints, the tendons, and the muscles, which do not normally arouse any conscious sensations through the cerebellum.

In discussing the physiological theories of the cerebellum we criticised that by which Ferrier maintains that it is the organ of unconscious equilibration. A similar theory has been put forward by other authors, on the strength of the experiments of Goltz, Breuer, and Brown, on the functions of the vestibular organs. On this theory the semicircular canals are the organ of the sense of equilibrium, or *static sense*, as others more vaguely term it. Nagel completely refuted this theory as follows:—

"It is certainly one of the functions of the labyrinth to maintain the equilibrium of the body in the different positions of rest and in locomotion. Its activity is expressed in the subconscious sensations of position and movement, and the reflexes necessary to keep up equilibrium. But these reflexes are not in any way specific to the labyrinth, since in this connection it always works with the organs of the so-called muscle sense. Every disturbance of the equilibrium of the body, when it leans to one side, involves abnormal relations of tension in the muscles, tendons, fascia, joints and skin, by which the afferent nerves of these tissues are excited, and which, with the express aid of the labyrinth, reflexly produce a movement in the opposite direction."

This co-operation of the labyrinth in the normal maintenance of equilibration as well as of orientation in respect of the vertical is obviously expressed in the reflex regulation of muscular tone, pointed out by Ewald. When the body leans to one side and is likely to fall, the passive movement excites the vestibular organs, and thus reinforces the tone of the muscles which move the body in the opposite direction. The movements of the eye which

accompany the compensatory movements must, according to Ewald, be considered as a special instance of corrective reflexes spreading over a large part of the musculature.

One last peculiarity remains to be noted in regard to the sensory functions of the non-acoustic labyrinth. As we have seen that under normal conditions the cerebellum is the seat of sub-conscious sensations, so the sensations of position and of normal movement normally aroused by the labyrinth in the cerebellum and bulb must be of the same kind when once it is admitted that this part of the brain contains its reflex centres. The sensations of rotatory and galvanic vertigo that can be experimentally produced in man by the methods of Mach and of Purkinje and Hitzig, and which are absent in deaf-mutes in whom the labyrinth is unable to function, are certainly not of this kind. They prove that the normally sub-conscious cerebellar sensations may, under certain experimental conditions, be so heightened and altered that they pass the threshold of consciousness and are clearly perceived in the form of rotatory vertigo and galvanic vertigo. This is an interesting complement to our own theory of the cerebellum, which is derived from the ingenious researches of the last twenty years into the physiology of the non-acoustic labyrinth.

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CHAPTER III

THE SENSE OF TASTE

CONTENTS.—1. Taste-buds the peripheral organs of the sense of taste. 2. Taste area mapped out by the physiological method of adequate stimuli. 3. Qualities of taste. 4. Mechanics of taste. 5. Correlation between the chemical and physical constitution of sapid substances and the intensity and quality of the excited tastes. 6. Inadequate stimuli; the so-called electrical taste. 7. Pathological alterations of taste-sense by disease or poisons. 8. Specific energies of the nerves of taste. Bibliography.

IN close relation with the sensations that can be aroused from the cutaneous surface is another series of specific sensations that originate in the ectodermal mucous surfaces of the mouth and nose. The Mouth is the seat of *gustatory*, the Nose of *olfactory* sensations. The sense of Taste enables us to recognise certain chemical qualities of the solid or liquid substances taken into the mouth as foods; that of Smell, certain chemical qualities of the gaseous substances that pass through the nasal passages along with the air inhaled.

Taste and smell are two specific and closely allied senses which may be termed *chemical senses*, not because their excitation is due to any definite chemical alteration in the corresponding sense-organs, but because the adequate stimuli for both these senses consist in special chemical substances that are soluble in water.

Taste and smell often function together, to such an extent that certain sensations which we locate in the mouth and call "taste" are proved by physiological analysis to be due to the activity of the sense of smell.

From the teleological point of view both gustatory and olfactory sensations are specially co-ordinated for the control and selection of foods and beverages, while their seat at the cephalic end of the digestive and respiratory systems enables them to act together and to arouse complex sensations, made up not merely of the elementary sensations of taste and smell, but also of the sensations excited in the tactile, thermal, and algesic organs with which the oral and nasal mucous membranes are richly provided.

1. The organs of taste are principally located in the depth of the stratified epithelium of certain parts of the dorsum and sides of the tongue—the organ which comes into immediate contact with the food, owing to the part it plays in the mastication of solids and deglutition of fluids.



FIG. 51. Papillary surface of the tongue, with the fauces and tonsils. (Sappey.) 1, Circumvallate papillae; 2, foramen cæcum; 3, fungiform papillae; 4, filiform and conical papillae; 5, transverse and oblique sulci; 6, mucous glands and lymphatic follicles at base of tongue and on fauces; 7, tonsils; 8, tip of epiglottis; 9, fraenum epiglottidis.

The anterior two-thirds of the tongue (Fig. 51) are covered on the dorsal surface, tip, and edges with a mucous membrane richly supplied with papillae visible to the unaided eye. The circumvallate papillae, 7-12 in number, can be distinguished at the border between the two anterior thirds and the posterior third of the tongue, and form the lingual V: the fungiform

papillae, much more numerous and smaller, are disseminated all



FIG. 52.—Semi-diagrammatic drawing of section of a fungiform papillae *a*, and four conical papillae *b*, of mouse's tongue (Fusari and Panasci); *c*, taste-buds; *d*, fibres of deep nerve plexus; *e*, group of nerve-cells; *f*, terminal fusiform swellings.

over the dorsal surface of the tongue, but are more numerous and

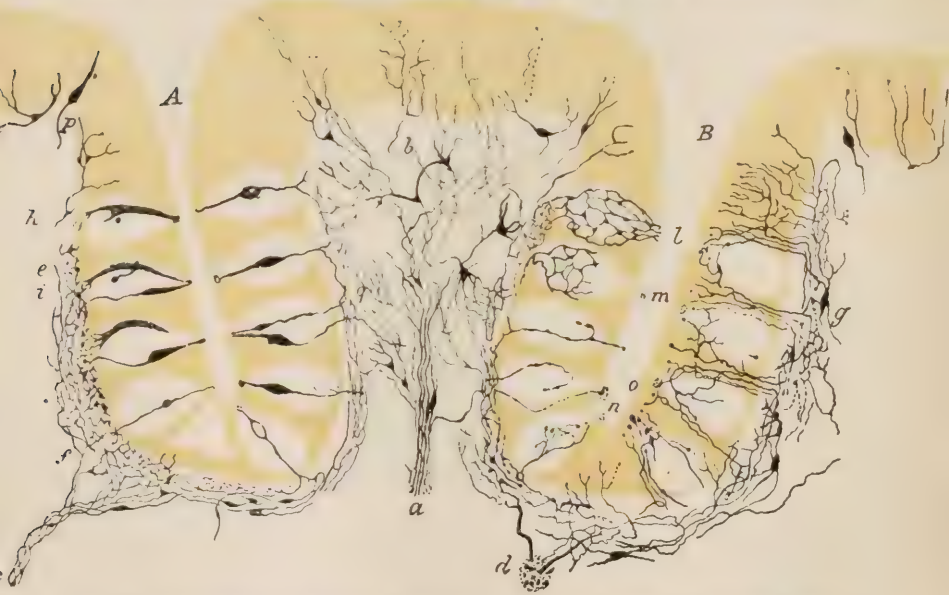


FIG. 53.—Semi-diagrammatic drawing of circumvallate papillae of mouse. (Fusari and Panasci.) The taste-buds and sustentacular cells of different shapes are shown round the depression *A*; the different forms of nerve-endings in buds and epithelium are shown round depression *B*. *a*, central nerve bundle; *b*, plexus of papilla; *c*, plexiform nerve bundle running to serous glands; *d*, lateral nerve bundle cut across; *e*, granules; *f*, nerve-plexus of granules; *g*, nerve-cells; *h*, *i*, sustentacular cells of taste-buds; *l*, *m*, peribulbar nerve networks; *n*, fibres of buds dividing and ending in tufts; *o*, inter-epithelial nerve-endings; *p*, terminal fusiform ramifications.

run together at the tip and sides; the conical and filiform

papillae, most numerous and smallest of all, cover the greater part of the dorsum of the tongue, but disappear towards its base. These papillae are comparable from the genetic point of view with those of the skin, and produce the rough, velvety appearance that characterises the dorsal surface of the tongue.

At the base of the circumvallate or fungiform papillae there are a number of serous glands which for the most part open into the fossae of the papillae and are absent in the rest of the mucous membrane.

All the circumvallate papillae and most of the fungiform are endowed with a specific gustatory capacity; in the more numerous conical or filiform papillae it is entirely lacking.

The gustatory sensibility of the circumvallate and fungiform papillae is due to the fact that they contain within their stratified epithelium the peripheral organs of taste known as the *taste-buds* or *bulbs*, discovered almost simultaneously by Lovén and by Schwalbe (1867). As shown by Figs. 52, 53 the taste-buds in the fungiform papillae lie in the axis of the papilla; in the circumvallate papillae they are arranged serially on the lateral surface of the mucous membrane and in the fundus of the fossae, and are usually absent in adults on the edges of these and on the surface of the papilla.

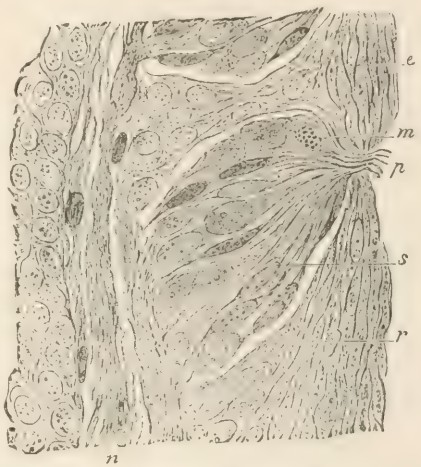


FIG. 54.—Section through taste-bud of papilla foliata of rabbit. Highly magnified. (Ranvier.) *p*, gustatory pore; *s*, gustatory cell; *r*, sustentacular cell; *m*, leucocyte containing granules; *e*, superficial epithelium cells; *n*, nerve-fibres.

Each taste-bud, examined histologically, consists of specially modified epithelial cells which together constitute a pear-shaped organ, 71-81 μ in height, and about 40 μ wide, which occupies nearly the whole depth of the ordinary stratified epithelium (Fig. 54). They contain two kinds of cells, of which one, known as supporting cells, form a compact layer at the periphery of the organ: these are inserted at the base of the taste-bud by one or more protoplasmic processes, and become smaller at the periphery where they are arranged so that the points turn towards the opening of the pore or bud. The gustatory cells contained in the axis of the bud are more slender than the supporting cells, their nuclei are smaller and slightly longer, and they have at the peripheral end a filiform appendage, the so-called *taste-hair*.

The hairlets of a taste-bud unite within the pore into a small brush that projects on to the surface of the mucous membrane.

In the depth of the taste-bud there are a certain number of non-medullated nerve-fibres, which are distributed as an arborescence between its cells (intragemmal or intrabulbar ramifications) and also between the cells of the papilla round the bud (intergemmal



FIG. 55.—Cells from taste-buds of rabbit. $\frac{1}{12}$. (Engelmann.) *a*, four gustatory cells; *b*, two gustatory cells and one sustentacular cell; *c*, three sustentacular cells.

or peribulbar ramifications). Some authors (Fusari and Panaschi) stated that the gustatory cells are in direct communication with nerve-fibres and thus form the cells of origin of the peripheral nerve-fibres (as occurs for the olfactory mucous membrane, *infra*). But the latest researches of Retzius and Lenhossék confirm the conclusions of Sertoli (1673) and Krohn (1875), that the nerve-fibres are merely in simple contiguity with the epithelial cells of the taste-bud, and penetrate between and branch round them (Fig. 56).

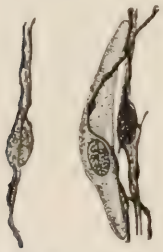


FIG. 56.—Two isolated gustatory cells and one sustentacular cell from a taste-bud, the nerve-endings terminating among them in club-shaped bulbs. (Arnstein.)

The nerve bundle that penetrates the bud, and the fibres that run to the flat epithelium of the papilla, come from a very fine sub-epithelial nerve-plexus which contains numerous small cells of a neural character, although this has been contested by some authors (Figs. 52, 53). This plexus receives nerve-fibres from a second plexus at the base of the papillae, which is formed from the fibres of the glossopharyngeal and chorda tympani nerves. This second plexus contains ganglion cells of different forms, some of which are in relation with the cervical nerves, others with the sympathetic system. The work of Kiesow and Nadoleczny and of Schlichting has recently confirmed the fact that the chorda tympani contains gustatory fibres.

That the taste-buds really represent the peripheral organs of taste is proved by the fact that they lie in the oral cavity, and in those papillae alone from which taste sensations can be excited,

while in other parts of the buccal and lingual mucous membrane where there is no sensibility for taste, nerve-endings similar to those we have described for cutaneous sensibility are very abundant.

These observations are confirmed by the fact brought out by von Vintschgau and Hönigschmied that after unilateral division of the glossopharyngeal nerve, which as we saw in the last volume (III. p. 401) is probably the only specific nerve of taste, one half of the taste area of the tongue becomes anaesthetic to taste, and after about four months the corresponding buds disappear, their elements being replaced by ordinary epithelial cells. All doubt as to the functions of these organs was removed by the

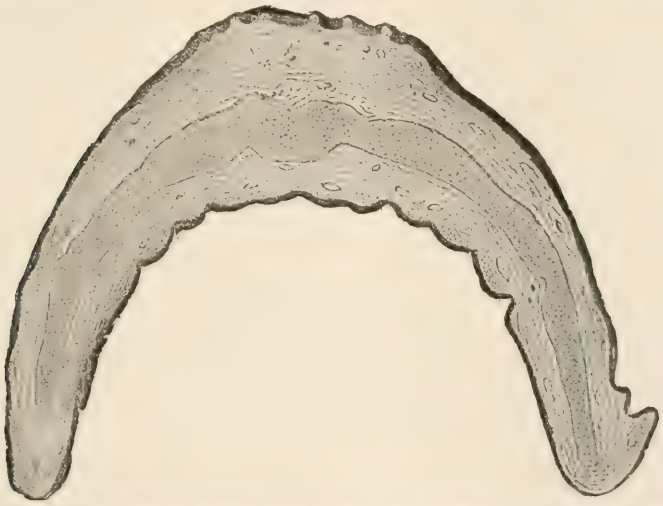


FIG. 57.—Transverse section of epiglottis of a human foetus at seven months (male). (Kiesow.) The taste-buds are shown on the surface of the tongue.

experiments made by Kiesow, with Hahn, on the taste sensibility of the human larynx.

The taste-buds are found not only in the anterior two-thirds of the tongue but also in the mucous membrane of the posterior third as far as the epiglottis, in the portion of the soft palate that lies above the uvula, in the anterior pillar of the fauces, in a portion of the posterior wall of the pharynx, and lastly in the anterior or lingual and the posterior or laryngeal surface of the epiglottis, and on the inner surface of the arytaenoid processes of the larynx (Fig. 57).

All other regions of the oral mucous membrane—the median part of the dorsum of the tongue, the lips, hard palate, uvula, tonsils, cheeks, and lower surface of the tongue—are normally destitute of taste-buds.

Finally, it is worth noting that during development the number of taste-buds continually decreases. In fact it has been demonstrated that in children the median portion of the dorsum of the tongue, as well as other regions of the oral cavity, are provided with taste-buds, and therefore with gustatory sensibility. This was first discovered by Urbantschitsch and subsequently confirmed by Kiesow, Stahr, and others. Stahr found forms of gustatory papillae in the centre of the infant's tongue that entirely disappear later on. Ponzo made further histological researches under Kiesow, and found taste-buds in the human foetus on the anterior and posterior pillars, as well as in the epithelium that covers the palatine tonsil and the mucous membrane that covers the nasal surface of the lateral parts of the soft palate. The taste-buds there are borne on high compound papillae, characteristic of this kind of mucous membrane, which has a stratified, ciliated cylindrical epithelium (Figs. 58, 59).



FIG. 58.—Compound papilla from dorsal part of soft palate of a human foetus (female) at term, with a taste-bud on the left side. (Ponzo.)

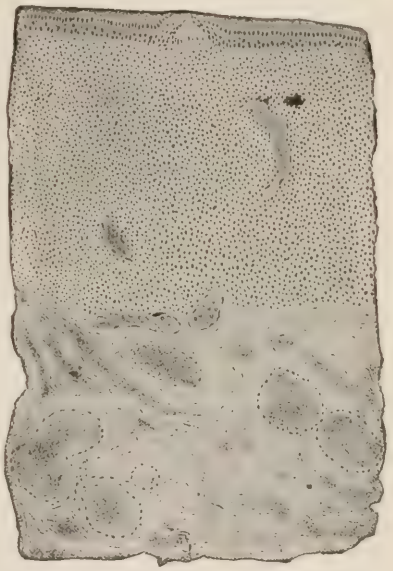


FIG. 59.—Nodule of adenoid tissue from the lateral wall of the nasal pharynx, near mouth of Eustachian tube, in human foetus (female) at term, with taste-bud. (Ponzo.)

Ponzo has also demonstrated the existence in the new-born of taste-buds in the pharyngeal part of the larynx, cervical part of the oesophagus, and the hard palate. His discovery in the new-born infant of taste organs upon the plicae fimbriatae of the tongue is important in phylogenesis, as they are more developed than in the adult, and must be considered as a vestige of the inferior accessory tongue of the pro-simians and of certain apes, in its turn a rudiment of an earlier form of non-muscular tongue (Gegenbaur). According to Giacomini this is more constantly present and even better developed in the negro race than in our

own. In all probability these organs are to some extent preserved, and the gustatory sensibility that Kiesow noted experimentally in some adults and still more in infants may depend on their presence.

II. Physiological exploration, by means of solutions of the different sapid substances which are adequate stimuli of the gustatory organs, is an even simpler method for determining the topography of taste and an approximately exact localisation of the taste-buds of the oral mucous membrane, but its application offers not a few practical difficulties which may be removed by the following precautions:—

(*a*) The gustatory mucous membrane of the oral cavity is also provided with delicate sensibility for touch, temperature, and pain. It is therefore necessary to select as stimuli specific gustatory solutions of such constitution and temperature that other forms of sensation are only slightly or not at all affected.

(*b*) Many substances that seem to be gustatory are mainly or exclusively olfactory; we must consequently select as stimuli such sapid substances as have no action upon the olfactory organ.

(*c*) The great mobility of the tongue and the diffusion of the substances applied to the surface of the buccal mucosa give rise to errors in estimating the extent of a taste area. It is essential that the subject should not move the part experimented on before he perceives the sensation. It is further necessary to distinguish the *immediate* and the *delayed* responses given by the subject. The former prove that the part explored is really gustatory, the latter are doubtful because the sensation may be due to spread of the test substance.

(*d*) It is possible that a given taste may be perceived in some regions and not in others which none the less form part of the gustatory area. It is therefore necessary to explore each part methodically for each quality of elementary taste.

Before so many precautions were taken gustatory sensibility was usually attributed to almost the whole of the oral cavity and a considerable portion of the pharynx. But when the above rules were observed the extent of the gustatory area became restricted by degrees to the limits now accepted by nearly all physiologists. It cannot, however, be denied that there are divergences between the different observers, which probably depend on individual differences in the distribution of the end-organs of taste.

In investigating gustatory sensibility it is usual to adopt either sapid substances or the galvanic method. Aqueous solutions of sapid substances are brought into contact with the oral cavity by means of small sponges fixed to the end of a wooden or metal rod (Verniere, 1827). Soluble solid substances may be applied directly by a brush (v. Vintschgau). When single papillae or inter-papillary spaces are to be tested all physiologists now prefer Ochrwall's method, *i.e.* the use of tiny brushes with blunt points saturated with the solution. In testing extensive surfaces diffusion of fluid

can be avoided by employing discs of gelatin or elder pith with a surface of the desired form, impregnated with the solution (Zwaardemaker, Quix). Kiesow stained his fluids slightly, to avoid the errors that may arise from diffusion.

In making a methodical research it is well to have a series of substances corresponding with the primitive tastes. Sugar can be used for the sweet tastes, quinine for the bitter, common salt for the saline, hydrochloric or sulphuric acid for the sour taste. Concentrated stock solutions can be kept of all these substances, from which solutions of different strengths can be prepared at any moment. Kiesow (1894) and Hänig (1901) used the following solutions for their important researches in Wundt's laboratory—sugar 10 per cent, hydrochloric acid 0·2 per cent, quinine sulphate 0·1 per cent.

The mode of application differs according to whether the taste-property of a certain substance is to be tested, or if it is desired to map out the sensibility to taste with the oral mucous membrane. In the first case it suffices to pour a given amount (about $\frac{1}{4}$ c.c.) of the chosen solution on the tongue, at a temperature of about 37° C. The subject then withdraws his tongue and applies it to the palate, and has to say immediately whether the solution has any taste, and if possible, what the taste is.

He must not know beforehand what substance is being used. The mouth must be rinsed with distilled water before passing from one substance to another. The sensation aroused by one substance must have entirely disappeared before proceeding to the next. This requires about five minutes. If the titration of the respective solutions is known, it is easy to determine the liminal stimulus, that is the minimal quantity of the substance that can arouse a definite sensation.

The above rules and precautions must be observed whenever the taste sensibility in the oral cavity is to be mapped out. In every experiment it is essential to find the liminal value for each individual and for each substance, *i.e.* the weakest solution that can be appreciated as taste in general or as a specific taste. It should be noted that with increased concentration of the solutions of some substances the quality of the taste alters as well as its intensity.

In order to control the veracity of the subject's judgments, and to test his attention, pure distilled water can be used on the brush at the outset or occasionally during the experiment.

Physiological investigation confirms our daily experience that the tongue is the principal organ of taste sensibility, but other areas, even beyond the oral cavity, are capable of perceiving taste. In children, as we have seen, the central part of the dorsum of the tongue is gustatory, but ceases to be so after a certain age: we must now discuss the localisation of the taste sense in adults, on whom it has been studied more accurately.

Every one admits, in accordance with the facts of histology, that the mucous membrane of the lips, gums, inner surface of the cheek, hard palate, lower surface of the tongue and central part of the dorsum are insensitive to taste. The evidence is less positive in regard to the tonsils and anterior and posterior pillars of the fauces, in which there are marked individual differences. According to Hänig these regions are sensitive to taste stimuli; according to Kiesow they are usually insensitive, particularly the posterior pillars. As regards the uvula the results were contradictory, owing to the rapidity with which the solutions diffuse.

To obviate this, Kiesow and Hahn employed a special spoon filled with a test solution which they introduced into the mouth after depressing the tongue with a spatula, and bathed the uvula in it. This experiment performed on sixty individuals showed the uvula to be insensitive to taste. Kiesow came to the same conclusion from his histological researches. The soft palate and posterior part of the fauces, on the contrary, possess a certain degree of gustatory sensibility (Kiesow and Petersen).

The discovery (referred to above) of taste-buds on the lower surface of the human epiglottis (Verson)—and on the lingual surface of this organ in the foetus, and in one case in a subject nineteen years old (Kiesow), and in the mucous membrane of the arytenoid cartilage of the larynx (Davis)—is surprising, and these regions were also found to be sensitive to different sapid substances (Gottchau, Langendorff and Michelson, Kiesow). The significance of this fact is not yet known. According to Kiesow these must be phylogenetic vestiges, possibly still capable of function, and concerned in the reflex coughing when sapid substances enter the larynx; according to Zwaardemaker these regions may possess gustatory sensations to gases, the so-called nasal taste—but on this point Kiesow expresses himself with reserve. That this effect, perceived on inhaling gases, cannot be referred to the mucous membrane of the nose seems positively proved by the careful investigations of Rollett.

Although it is the principal seat of taste the tongue is incapable of perceiving flavours at all points of its surface. The region of the circumvallate papillae is very sensitive, and from this region the gustatory area extends along the margins of the organ to the tip. Beyond the lingual V the individual variations in the distribution of the end-organs of taste are remarkable, not only as regards their anatomical localisation, but also in the quality of the tastes perceived.

In adults a large oval area in the most central part of the dorsum of the tongue, some 3 cm. wide and of variable length, is insensitive to taste.

The statements refer to taste sensibility in general; but the capacity of perceiving the quality of tastes does not seem to be distributed equally over the surface of the tongue. This fact, already known to the earlier observers (Horn 1825, Guyot and Admirauld 1830), was subsequently confirmed and better defined by other workers. The differences are particularly conspicuous when the base and the tip of the tongue are examined separately. Thus, according to Rouget, sodium chloride, which has a purely saline taste on the front of the tongue, is slightly bitter if applied to the V, and the same is true of nitrate and acetate of potassium. According to Lussana, potassium chloride and sodium sulphate have a saltish taste on the tip of the tongue: while the former is

sweetish, the latter is bitter at the base; alum, on the contrary, is acid at the tip and sweet at the base. The number of substances that taste differently at the two ends of the tongue are continually being added to. Bromo-saccharine (Howell and Kastel), which tastes sweet at the apex and bitter at the base, is typical. The tip of the tongue is, however, able to perceive the bitter taste of quinine and of many other substances. Generally speaking, it may be said that every part of the tongue that is provided with taste-buds can distinguish the primitive qualities of taste; but there are distinct differences in sensibility between the different points of the tongue.

The latency of sensations to various tastes is also different at the apex and the base. This fact, demonstrated by v. Vintschgau and Hönigschmied, was confirmed by others, as shown by the following table:—

	Sodium Chloride. sec.	Sugar. sec.	Quinine. sec.
Tip of the tongue . . .	0·597	0·752	0·993
Base of the tongue . . .	0·534	0·552	0·501

The dissimilar capacity of the base and the apex of the tongue in appreciating tastes has been referred to the different origins of the nerves that supply these regions, but although the lingual nerve ramifies in the anterior part of the tongue, and the glosso-pharyngeal in the base, the gustatory fibres of the lingual probably come from the glosso-pharyngeal (Vol. III. pp. 401-5). It seems probable, therefore, that these differences are accounted for by the fact that the specific organs for the several tastes are unequally distributed over the different gustatory regions of the tongue.

Kiesow, by an exact method, obtained the following reaction times for the tip of the tongue alone:—

	sec.
Sodium chloride	0·308
Sugar	0·446
Hydrochloric acid	0·536
Quinine	1·082

He points out that these values agree perfectly with the general fact already established by Schirmer, that in a mixture of the four sapid substances applied to the tongue salt is appreciated first, then sweet, thirdly acid, and lastly bitter.

According to Schreiber (1892) the insensitive central area on the dorsum of the tongue varies in extent according as sweet, acid, salt or bitter substances are employed. As shown by the diagram (Fig. 60) the area insensitive to acid is the smallest, to bitter the most extended. The area that is insensitive to acid is insensitive also to almost all other tastes. But we must not assume this to be a general rule; without criticising the method employed by

Schreiber, we must remember that his results were obtained from one individual only. According to v. Vintschgau and others, the four qualities of taste cannot be distinguished equally well by all persons at the tip of the tongue. Some find difficulty in distinguishing the different tastes; others can only discriminate between certain of them; in others again the tip of the tongue is insensitive to all tastes. At the base, on the contrary, every one is normally able to distinguish the primitive qualities of taste.

The methodical exploration of the whole surface of the tongue made by Kiesow (1894) in Wundt's laboratory altered the somewhat vague and uncertain ideas that prevailed on this subject. According to Kiesow the tip of the tongue is most sensitive to sweet tastes, acid is best perceived at the sides, bitter at the base, while the sensibility to salt is approximately equal over the whole gustatory surface, though somewhat less at the base than at the apex and sides. Kiesow further established that sensibility to salt is practically the same in different individuals, and that where individual differences occur they are insignificant.

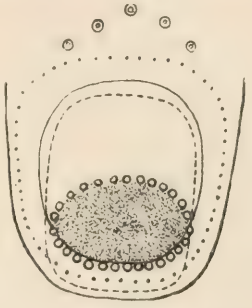


Fig. 60.—Diagram of region which is insensitive to various tastes on the dorsal surface of the tongue. (Schreiber.) The finely dotted oval area is insensitive to all tastes; the area surrounded by an unbroken line is insensitive to sweet; by a broken line to salt; by a dotted line to bitter; by a line formed of small circles to acid.

The portion of Kiesow's work that bears on our present subject was resumed by Hänig (1911). While Kiesow had confined himself to determining the sensibility of the different lingual gustatory regions on the tongue, Hänig, continuing this research, established *isogustatory* zones with parallel margins, which he terms *isochymes* for the whole gustatory area, and carefully investigated the exact liminal value of the sensory points in each zone. The different sensibility to the four primitive tastes in the different gustatory regions of the tongue is shown in different colours in Fig. 61. A glance at Hänig's diagram brings out the following important facts, which, on the whole, confirm those discovered by Kiesow:—

(*a*) Sensibility to *sweet* is greatest at the tip of the tongue, least at the base. Sensibility to this taste diminishes not only from the tip along the edges of the tongue, but also centripetally from the periphery towards the oval central zone, which is insensitive to taste.

(*b*) The maximal sensibility to *bitter* lies in the region of the circumvallate papillae, its minimum at the tip of the tongue and at the neighbouring portions of its edge. The capacity of perceiving this taste diminishes rapidly at first from the base to the

tip, afterwards more slowly, while there is a gradual diminution from without inwards.

(*c*) Sensibility to *acid* is maximal in the median part of the border of the tongue, and diminishes towards both base and apex, and from without inwards towards the central anaesthetic zone.

(*d*) Sensibility to *salt* is maximal at the apex and margin of the tongue, minimal at the base. From both the apex and the base it remains approximately constant up to the anaesthetic region, and only diminishes perceptibly in the lateral portions.

These conclusions, at least in so far as concerns the general

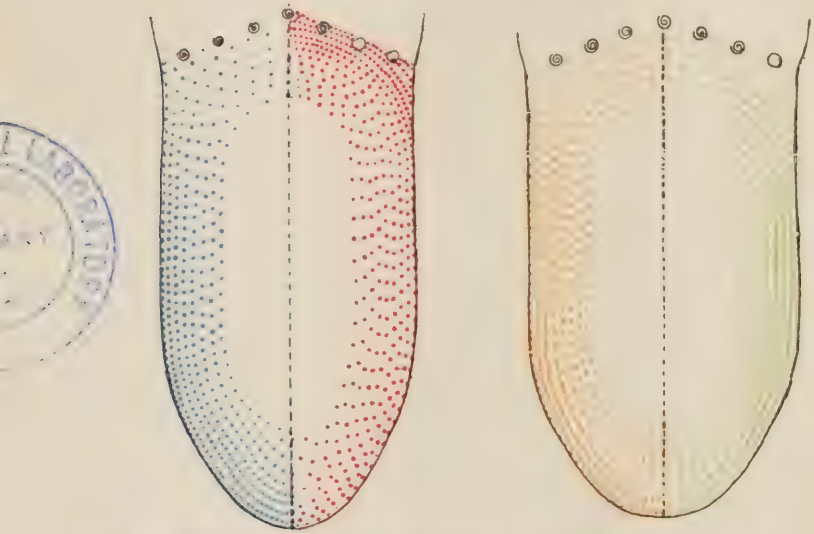


FIG. 61.—Diagram of topographical distribution of gustatory sensibility to the four primitive qualities of taste on the dorsal surface of the tongue. (Hänig.) The sensory spots for each of the four qualities of tastes are arranged in parallel isogustatory lines (*isochymes*). Those for sweet (marked blue) are most dense at the apex of the tongue; those for bitter (red) at the base; those for acid (green) at the borders; those for salt (yellow) at the borders and tip of the tongue.

topography of the taste sense in the tongue, are confirmed by the fact that they agree essentially with the early observations of Guzot and Admirauld (1830), and of Stich and Klantsch (1858), as well as those obtained by Rosenthal (1860) and Neumann (1864) with galvanic stimulation.

In infants, as has been said, the whole surface of the tongue is sensitive to taste, and has no anaesthetic zone such as is constantly present in adults. To account for the change, Kiesow assumes that in adults it is more necessary to have the control of taste in the marginal portion of the tongue which is nearer the teeth, the instruments of mastication, while the sensibility of the central area of the tongue in early life is correlated with the

requirements of sucking and of liquid alimentation in general. Moreover, the penetration of liquids into the pores of the taste-buds is facilitated in adults by the mechanical compression of the tongue against the teeth and jaws.

But how are we to explain the different distribution of specific sensibility for the four primitive tastes? No definite answer to this is possible. Kiesow, however, assuming a hereditary tendency, holds that the taste organs found in the tongue are specially adapted to external stimuli. He notes the tendency to keep substances that have a pleasant taste longer in the mouth than those which give a disagreeable sensation, the latter being either spat out at once or swallowed quickly. Kiesow attributes the small difference in the sensibility to salt of different parts of the tongue in most individuals to the fact that the saliva of the oral cavity, at least of its anterior part, is approximately equally distributed and everywhere has the same content of salt. It should also be noted that Wundt sees a close relation between these facts and certain mimic facial movements.

III. An exact distinction and classification of the qualitative differences of tastes, *i.e.* the qualities of the specific gustatory sensations excited by sapid substances in the peripheral organs of taste, is only possible by the *sensorial method*—that is, by subjective appreciation of the fundamental or specific differences in the different sensations of taste. As we are almost completely ignorant of the chemical or physical properties which enable certain substances to excite the peripheral organs of taste, we cannot base any classification upon them.

In daily life we make a distinction between the sapid substances, based on the affective impression they make upon us rather than on the quality of their tastes: thus we discriminate between agreeable, indifferent, insipid, and disagreeable tastes. Agreeable and disagreeable substances excite different expressional movements of the facial muscles; indifferent and insipid substances produce no facial movements, or at most arouse an expression of indifference or slight disgust. These reactions may be considered as instinctive reflexes, because they are involuntary; they were even noted by Sternberg in an anencephalic foetus.

By means of these expressional reactions it is possible even in babies of a few months old and in many animals to distinguish clearly between the sensations aroused by different tastes in the mouth. A sweet taste always gives them a pleasurable sensation, even when it is in excess. Other substances, on the contrary, give a disagreeable sensation in concentrated solutions, or are indifferent if very dilute. In the first case the reaction is a movement of sucking or licking; in the second there are efforts at repulsion and evidences of displeasure or disgust.

In adults there is less predilection for sweet things, and a

tendency develops to find pleasure in many other simple or compound tastes, acid, bitter, or salt, so long as they are in weak or moderately concentrated solutions. But the more or less pleasant or unpleasant character of different flavours varies according to the individual, and is in no necessary relation to the nocuous or innocuous effects of the various foods. The proverb that "what is good to eat can do no harm" only holds for those food-stuffs that have already been physiologically selected.

The affective tone concomitant with the taste sensations must be carefully distinguished from those qualities of taste which we perceive as a property of extraneous substances by which the gustatory surface is specifically stimulated.

In addition to the four primitive tastes we have been discussing—sweet, bitter, acid, salt—we commonly speak of a great many other tastes by specific names, *e.g.* alkaline, metallic, astringent, acrid, sharp, aromatic, alcoholic, fatty, slimy, dry, etc. Most of these tastes, however, are found on physiological analysis to be compound, *i.e.* they consist of several elementary constituents, in which the sensations of taste are mingled with olfactory sensations, and with the tactile, thermal, and pain sensations which are well developed in the mucous membrane of the mouth.

Chevreul (1824) first noticed the ease with which gustatory sensations become associated with tactile and olfactory sensations, owing to the great delicacy of tactile sensibility in the tongue and the acute olfactory sensibility of the adjacent nasal mucous membrane. Few substances are indifferent to the tactile and thermal, sensory nerve-endings of the tongue, and so entirely destitute of olfactory properties as to be unappreciable by smell.

Physiological analysis enables us clearly to distinguish the purely elementary qualities of taste in the innumerable gastronomic flavours.

It is easy to separate smell from taste; if the nostrils are closed, the aromatic, alcoholic, or nauseous flavours disappear. The same occurs when olfactory sensibility is abolished by a violent cold. In making a methodical experiment it is well to blindfold the subject as well as to close his nose, to avoid visual suggestion. It is then impossible by taste alone to distinguish the aromas of different wines, of coffee, tea, chocolate, oil and butter, various kinds of meat (Wing, Longet, Béclard), the alkaloids, such as aconitine and nicotine (Richet and Gley), etc. But even after absolute exclusion of smell the perception of the four tastes known as primitive, *i.e.* sweet, bitter, acid, salt, remains unchanged.

The devices for separating thermal, tactile, and pain sensations from those which are purely gustatory are more elaborate. To exclude complication by thermal sensations, which introduce a character of hot or cold, it suffices to warm the test solution to

body temperature. Tactile sensibility can be excluded by applying the substance in solution not as a solid or powder, so as to avoid any mechanical stimulation of the touch spots. To distinguish the sensations excited through the pain organs from taste, it is necessary to compare the effect of the solutions on those parts of the oral cavity that have and have not taste-buds—the latter being the inferior surface of the tongue, mucous membrane of the gums, cheeks, hard palate, and centre of the tongue. By this means it is found that the attributes sharp, astringent, oily, dry, etc., as applied to tastes, are due exclusively to the general sensibility of the oral mucous membrane, particularly that of the tongue. All these sensory attributes are in fact produced when the test solutions are applied to the mucous surfaces that are destitute of taste-buds, but no pure gustatory sensations (sweet, sour, bitter, salt) are thus excited.

Zenneck (1839) only admitted two qualities of purely gustatory sensation, sweet and bitter. Valentin (1848) maintained the same. More recently (1883), M. Duval went even further, and asserted that taste sensibility was intermediate between common sensibility and specific sensibility, and that many sensations aroused on the tongue might equally be evoked from other mucous membranes and on certain parts of the skin.

On the other hand, the careful observations of Stich (1857) showed that the acid taste is not diffused over the whole of the buccal mucosa, but only when there are taste papillae. Schiff (1867), again, found that where the epidermis had been removed by a blister, the application of solution of sugar, quinine sulphate, or citric acid gave rise to different sensations which bore no resemblance to taste. He also found that any highly diluted acid which produced no sensation on the non-gustatory mucous membrane of the mouth was clearly perceived in the gustatory parts of the tongue. Fick (1864), on the contrary, showed that acids only excite the nerves of pain in concentrated solutions. This agrees with v. Vintschgau's observations of 1880, that salt solutions, sodium and ammonium chloride, and potassium iodide could only act on the non-gustatory mucosa in concentrated solutions, while in dilute solutions they are perceived solely in the taste area. Kiesow (1894) showed that not only salt and acid, but sweet and bitter as well, are accompanied by tactile sensations, which in the highest degree of sweetness may become very intense.

From this it may be concluded that acid and salt, as well as sweet and bitter, are true tastes. Nevertheless, Rouget (1875) and Lannegrace (1878) admitted sweet and bitter alone to be true tastes, and held that acid and salt were pseudo-tastes or chemical taste sensations. This refinement, however, has no real foundation. In fact, these authors themselves recognised that "dilute solutions

of acid or salt applied to the tongue produce specific sensations which are not aroused from any other sensory surface, and which give particular information about these substances under the familiar name of acid or salt taste." This amounts to saying that acid and salt are true tastes, although, unlike sweet and bitter, they may be associated with general sensations when not sufficiently diluted.

Bain, Wundt, and others admit the alkaline and metallic also among the true tastes. It was long debated whether these two tastes should be admitted among the four generally recognised as primitive, or whether they should be considered as compound sensations due to the admixture of several tastes. Von Vintschgau recognised that the metallic taste excited by electrical stimulation of the tongue is very difficult to analyse, and that in alkaline and astringent tastes common sensibility plays such an important part that it is hard to know if the taste organs also are excited. Oehrwall holds that the alkaline taste results from the combination of many tastes, associated with sensations of contact. The researches of Kiesow and Höber led these authors also to the conclusion that the alkaline and metallic tastes depend on the association of several primitive gustatory sensations; that acid and sweet are components in a metallic taste; and that in an alkaline the general sensibility components are associated sometimes with bitter, sometimes with sweet.

Von Frey assumed that alkaline and metallic tastes are mixed sensations with an olfactory component. Herlitzka showed that the so-called metallic taste is neither a gustatory nor a mixed sensation, but purely olfactory. More recently v. Frey came to the same conclusion in regard to the alkaline taste.

Henle distinguished as insipid tastes the impressions produced by solutions that are poorer in salt than the saliva. The taste organs are so accustomed to the action of the buccal secretions that the latter are quite indifferent, as regards taste. But directly the concentration of these fluids is lowered, we become aware of a faint or indefinite sensation commonly known as *insipid*. A typical illustration of this is the sensation produced by distilled water, which is deprived of carbonic acid. According to Kiesow, a very dilute alkali also has an insipid taste, and a much diluted mixture of salt and sugar is insipid.

In conclusion, the usually recognised qualities of taste are reduced to four: sweet, bitter, acid, salt. These are primitive or elementary tastes, because they cannot be further analysed. If we make of substances belonging to each of these four groups solutions that will arouse equal sensations, we cannot distinguish between the sensations aroused, *e.g.* by hydrochloric, nitric, sulphuric, acetic, and oxalic acid. The same applies to the bitter substances, *e.g.* strychnine, quinine, digitaline, morphine,

picric acid, as also to sweet solutions, as sugar, glucose, and lactose.

IV. The relations between the nature of adequate thermal, tactile, auditory, and visual stimuli and the quality of the sensations aroused in consciousness are well known, but the same cannot be said of the chemical senses, taste and smell, since we do not yet know in what chemical property the capacity of certain substances to act as adequate stimuli for taste or smell consists. We only know a few of the conditions that determine the taste and odour of a substance. It is generally admitted that sapid substances are adequate taste stimuli only when in a state of solution. Formerly, however, it was believed that gases were also capable of directly stimulating the organs of taste (Joh. Müller, Stich). Carbonic acid has a distinctly sour taste; chloroform, sulphuretted hydrogen, and nitrous oxide are sweetish; aldehyde and ether vapour are slightly bitter; acetic acid vapour is strongly acid, and on excluding smell cannot be distinguished from some of the mineral acids. These tastes are distinctly perceptible, even when the substances are brought in the form of gas into direct contact with the tongue after drying it carefully, and closing the nostrils.

The direct action of gases was disproved (Valentin, von Vintschgau) by the fact that gases, before coming into contact with the specific taste-endings, are necessarily dissolved in the fluids which fill the pores of the taste-buds. It is consequently indisputable that substances, whether solid, liquid, or gaseous, must, in order to affect the peripheral organs of taste, be in the form of solutions, or be dissolved in the oral secretions. Solubility in the oral secretions, at least to a minimal extent, is therefore an indispensable condition of gustatory stimuli.

Compounds of the different metals, at the surface of which there is a difference in electrical potential, and which on contact with the tongue may give rise to electrical excitation of the taste-organs, form an apparent exception to this law.

On the other hand, solubility alone is not sufficient to enable a substance to excite sensations of taste. Some gases, *e.g.* oxygen, hydrogen, nitrogen, never arouse sensations of taste, though soluble in the oral secretions and absorbable. The same holds for distilled water, after carefully cleansing the mouth from the food residues and sapid substances mingled with the saliva. It is more surprising that chloride or sublimate of mercury, to which individual tissues are certainly not indifferent, has no taste in certain concentrations (Sternberg).

According to Graham sapid substances belong to the category of *crystalloids*, while *colloids* are tasteless. Although it is not easy to control the absolute value of this statement, owing to the difficulty of obtaining colloids in the pure state, and to the fact

that they become altered and decomposed on contact with the buccal secretions, the difference in the two classes of substances nevertheless indicates that to be capable of stimulating the organs of taste, all substances must be in a state of true and perfect solution; colloids only form pseudo-solutions, and exist in fluids in the form of groups of several molecules. As all food-stuffs except the sugars are insoluble in water, and therefore quite devoid of taste, it follows that the gustatory characters by which we are able to recognise food-stuffs in general (proteins, colloidal starches, fats) depend on the minute traces of soluble crystalloid and volatile substances mixed with them.

In order that the substances dissolved in water may come into contact with the nerve-endings of the taste-cells, it is necessary that they should first diffuse in the fluid contained in the pores of the taste-buds; this causes a certain delay in their chemical action, and possibly a certain temporary separation of the active components of the solution, if the rate of diffusion differs.

The taste papillae are so arranged that all substances introduced into the oral cavity in sufficient amount must come into contact with them. The roughness of the lingual surface owing to the projection of the papillae, and the numerous interpapillary depressions, are conditions that promote the retention of the solid and liquid particles in the interpapillary spaces and the diffusion of the dissolved substances to the gustatory pores.

The movements of the tongue increase the surface of contact between the organ of taste and the contents of the mouth. Fick held that these movements increased the excitability of the gustatory nerve-endings by mechanically stimulating the organs of taste. He went so far as to declare that the substances applied to the dorsum of the tongue when it is stationary are scarcely perceived or not at all. But the subsequent researches of Oehrwall and others disproved this statement and showed that the lingual movements merely increase the surface of contact between the active substance and the sense organs. At most it may be said that the pressure of the tongue against the hard palate facilitates the penetration of the fluids into the interpapillary spaces.

The salivation of the bolus, for reasons that can readily be appreciated, facilitates the solution, diffusion, and perception of the flavours of solid and semi-fluid substances. The secretion of the salivary glands and of serous glands that open into the fossae of the circumvallate papillae also exert a protective function upon the gustatory organs, because in the case of unduly strong tastes there is a reflex stream of buccal secretion which diminishes their action on the specific nerve-endings.

Haller assumed an erection of the lingual papillae in gustatory activity, but this is disproved by the observations of Bidder and Oehrwall.

V. What is the physical or chemical property that confers upon certain bodies the capacity of stimulating the taste organs? Why do some of them arouse a sensation of sweet, others of bitter, others of acid, others lastly of salt? Why do other substances that are equally soluble and diffusible remain inert as regards taste? These are the fundamental questions that arise when we attempt to determine the relations between chemical structure and the sense of taste.

At first sight it does not seem difficult to discover a series of correlations between the chemical composition of bodies and their taste. Almost all acids have a sour taste, many salts a salt taste, a large number of alkaloids are bitter, many carbohydrates are sweet. It might reasonably be supposed that some of the properties which enable us to classify these substances into definite and distinct chemical groups represent the cause or constitute the origin of their respective flavours. But this correlation is more apparent than real, because not all compounds chemically known as acids give an acid taste, not all salts a salt taste, not all alkaloids are bitter, nor are all sugars sweet. There are bodies of very different constitution from the sugars which arouse a sensation of sweetness, such as the glucosides, saccharine, chloroform, and certain mineral salts, as lead acetate and salts of beryllium. On the other hand, it is interesting to note that one sugar, *d*-mannose, has a bitter taste, while many other mineral and organic substances of varying chemical composition which do not belong to the alkaloids have the same bitter taste. Lastly, there are compounds of closely allied chemical composition, with different tastes. Such are the two asparagines (Piutti), of which the dextro-rotatory is sweet, and the laevo-rotatory tasteless, although they do not differ chemically, but only in their optical properties. These enigmatical facts have so far received no interpretation.

The first advance in the correlation of chemical structure and taste was made by the researches of Gley and Richet (1885), who compared the liminal values, as taste stimuli, of the chlorides, bromides, and iodides of different alkaline metals—lithium, sodium, potassium, rubidium—the atomic weights of which differ in the relations of 7, 23, 39, 87, although their chemical properties are very similar. They found that equimolecular solutions were required for liminal excitation of the taste organs, *i.e.* such as contained approximately the same number of molecules of the twelve different alkaline salts, whatever the absolute weight of these molecules. Hence, according to Gley and Richet, it is legitimate to conclude that their physiological action on the organs of taste is a chemical effect, because it takes place according to the laws of ordinary chemical action.

Another interesting series of researches into the gustatory property of acids was made by Corin (1888). He employed

equimolecular solutions of a great number of acids with the object of determining whether the intensity of the respective tastes is in any relation with their acidity in a chemical sense, that is with the amount of soda they are capable of neutralising. By patient research he arrived at the conclusion that the acidity of different equimolecular solutions of acids is so much the stronger in proportion as their molecular weight is lower, and that, generally speaking, the intensity of the acid taste of a molecule of any acid depends on the relation between the weight of the acid hydrogen (*i.e.* that which can be replaced by a metal) contained in the molecule and the weight of that molecule.

Another important question was attacked by Höber and Kiesow (1898): do substances soluble in water, or of which the molecules are capable of ionisation (electrolytes), owe their taste to the free ions or to the molecules that are not dissociated, *i.e.* are electrically inactive? Can free ions of different kinds give rise to different sensations of taste when they act on the gustatory organs? All these possibilities seem probable in view of the fact discovered by Höber and Kiesow, that a single salt solution may give rise to a whole series of gustatory sensations which differ not only in strength but also in quality.

We know by the laws that govern the dissolution or dissociation of salts that in solutions of minimal to medium concentration the cleavage of the molecules into kations and anions, respectively, is complete, and that it is only in more concentrated solutions that non-dissociated electrically inactive molecules are present. Höber and Kiesow studied the taste of certain saline solutions in relation to the different degrees of their ionisation, and recognised that the taste sensation aroused as a whole by the solution of an electrolyte (or ionisable salt) is the resultant of a certain number of different elementary taste sensations, which are severally excited by the ions.

Highly dilute solutions of alkalis which are completely or almost completely dissociated have a sweet taste; in stronger concentration they have a characteristic soapy taste, which is probably due to the unsplit molecules.

The salt taste of a series of salts (NaCl, KCl, $MgCl_2$, $(CH_3)NH_3Cl$, $(C_2H_5)NH_3Cl$, $NaBr_2$, NaI, K_2SO_4, Na_2SO_4) is due to the anions set free by the dissociation of the molecules. In other salts, on the contrary, the effect of the kations predominates, and there is no salt taste. This is the case with the salts of magnesium, which are bitter, and the salts of beryllium, which are sweet.

The work of Höber and Kiesow thus shows that three of the primitive qualities of taste, salt, sweet, and bitter, can be produced by the free ions. As Richard also showed that acidity is excited by hydrogen ions, we may conclude that all four

elementary qualities of taste can be elicited by the action of the ions on the gustatory nerve-endings. Höber and Kiesow believed that by comparing the tastes of the solutions of a great number of electrolytes the taste of many kinds of ions and molecules could be determined. But this would not explain the origin of the different qualities of taste, because nothing is known about the relation of the latter to the peripheral taste organs on which sapid substances act. Still it is shown by the work of these authors that the compound taste of many substances results from the sum of the tastes of their individual components, broken up by the dissociative force of the water.

Herlitzka arrived at somewhat different results. On examining the taste of over seventy salts he came to the conclusion that the taste of the salts was due to the free ions and not to non-dissociated molecules, and in confirming the conclusions of Richard and Kahlenberg that the acid taste is due to hydrogen ions, and of Höber and Kiesow that the salt taste is dependent on the anions, he affirms that the elementary kations (excepting, of course, the hydrogen ions) have a sweet or bitter taste, or both together. The taste of a salt would thus result from the conflict between the taste of the anions and of the kations, some salts having only the taste of one, some of the other, some of both.

Attempts have also been made to determine the relations between different tastes and the relative position of the atoms and the various groups of atoms in the molecule. We are mainly indebted to Haycraft (1887), Sternberg (1898–1903), and Herlitzka (1908–9) for these interesting researches.

Haycraft found that the molecular weight of a substance, even if it affects the *intensity* of a taste, has no important influence upon *quality* of the taste sensations. On the contrary, the different groups of Mendeléeff's system show a marked agreement in their gustatory qualities. The chlorides of the first group (Li, Na, K, Cu, Rb, Ag, Cs, Au) all have a salt taste, while the sulphates have a bitter-sweet taste. The chlorides of the second group (Mg, Ca, Zn, Sr, Cd, Ba) are bitter-salt, except the salts of beryllium. The chlorides of the seventh group (I, Cl, Cn, Br), again, have a bitter taste. Another fact discovered by Haycraft is that the organic compounds containing the group COOH have an acid taste; the alcohols, with the exception of the lowest members of the series, are sweet.

Sternberg, too, attempted to ascertain the relations between given groups of molecules and certain tastes. He called these groups *sapiforous*, and included in them the groups OH, NH_2, NO_3, which in various combinations of the organic molecules have different tastes.

Herlitzka took up the relations between the taste of the ions and their position in Mendeléeff's periodic system, and pointed

out that this relation, as expressed by Haycraft, must have been different if he had considered the taste of the salt as a whole, and not that of the kations. Herlitzka employed Ramsay's scheme to bring out the relation between the taste of the kations and their position in the periodic system. From his researches as a whole he was led to formulate the hypothesis that the excitation of the peripheral taste organs by means of the salts is produced (like the excitation of other elements of the body) by a change in the state of the colloids, with alteration of their electrical potential.

According to Herlitzka the metallic sensation (metallic taste, more correctly metallic smell) is characteristic only of a small number of salts, all belonging to the heavy metals; and that only when the metal is present in the form of elementary ions, never in the form of complex ions. With some metals, moreover, the metallic smell is perceived when they are present in the form of a certain ion, but is absent with forms of ions of a different valency. According to this author the threshold of stimulation for the metallic sensation is extremely low, and varies for the different salts between $\frac{n}{9000}$ and $\frac{n}{50,000}$: their solutions not only have no taste, but many of them do not give the characteristic reaction of the respective ions. In these the molecule is completely dissociated. For the salts of the weak acids in which the process of hydrolysis is more active, the threshold is slightly higher.

The metallic smell consequently appears to be a property of elementary, dissociated ions.

According to von Frey the alkaline taste (smell) depends on the liberation by the alkalis of the volatile bases (methylamine) that result from the products of the decomposition of the epithelium from their salts.

VI. Special attention should be paid to the fact that the end-organs of taste differ specifically from the other sense organs possessed by the tongue in common with the skin, in being incapable (so far as is known) of excitation by mechanical and thermal stimuli. Among inadequate stimuli of the taste sense we need therefore only consider the action of the electrical current.

Sulzer (1752) first noted that on applying two different metals to the tongue a special gustatory sensation resulted which he compared to the taste of rust. Volta (1792) repeated Sulzer's experiment without knowing of it, and found that the special taste was due to the passage of an electrical current; in fact he obtained the same effect on stimulating the tongue with the current from his pile. Volta inclined to the opinion that the electricity acted directly upon the taste organ. A few years later Humboldt (1797) suggested that the electrical taste was

due to the products of the chemical decomposition produced in the tongue by the passage of the current. These divergent opinions gave rise to two theories which for a century disputed the effects of the electrical current on the organ of taste.

Humboldt's explanation assumed a more definite form when it became known that the passage of an electrical current through a solution of alkaline salts (such as the buccal secretion) caused its electrical decomposition, so that acid was liberated at the anode and alkali at the kathode. This fact is sufficient of itself to explain why, on passing a galvanic current through the part of the tongue that is supplied with gustatory sensibility, there is an acid taste on applying the anode (the kathode being placed on the neck or some other part); when the kathode is applied to the tongue there is, on the contrary, an alkaline taste.

But this explanation is opposed by an ingenious experiment made by Volta and confirmed at a later date (1860) by Rosenthal. If the tip of the tongue is dipped into a small tin vessel filled with an alkaline solution, and held in the moist hands so as to produce a weak current, the acid taste is equally perceptible. If this taste depended on electrolytic action it ought not to appear under these conditions, because the acid would at once be neutralised by the alkali in the vessel.

Rosenthal adduced other experiments in support of Volta's opinion. If two persons are in circuit by means of placing the moist hand of one on the positive pole and of the other on the negative pole of an electric battery, and the tips of their tongues are brought into contact, the first will be aware of an acid taste, the second of an alkaline. Both tongues are under identical conditions, being separated only by a thin layer of buccal secretion, and the sole difference is the direction of the current passing through them. How then can there be an alkaline fluid on the one side and an acid on the other at the point of contact of the two tongues? Rosenthal also experimented on the stimulation of the tongue by an electrode formed of red litmus paper, which became blue on contact with the buccal fluid, before the passage of the current. During the passage of the current when the paper acted as anode, the subject perceived the characteristic acid taste, but the paper did not turn red, showing that no perceptible amount of acid was liberated at the anode.

Hermann objected to the first two experiments that electrolytic decomposition might take place in the depths of the lingual tissue and not at its surface; for the third it was remarked by Valentin that the taste-endings might be more sensitive than litmus paper.

But there are other points in connection with the electrical taste that claim attention. Ritter (1798) stated that on passing an electrical current for a long time through the tongue,

the electrodes being at a certain distance from each other, and on then breaking the current, the original acid taste at the anode became first slightly bitter and then alkaline, while the alkaline taste at the kathode simultaneously became acid.

These observations were repeated and confirmed with variations by Hermann and Laserstein (1891), Shore (1892), and Hofmann and Bunzel (1897). Hermann and Laserstein showed that it is not the oscillations in the intensity of a constant current but the current itself which produces the electrical taste. The comparatively weak effect of induced currents is due to their brief duration. On applying the anode to the tongue there is a decidedly acid taste during the passage of the current; on applying the kathode the taste becomes alkaline. But the acid taste is more pronounced than the alkaline, and is not neutralised by alkaline fluids. On breaking a weak galvanic current there is an acid after-taste even when the taste has been only slightly alkaline during its passage. Shore obtained similar results.

Hofmann and Bunzel stated that when the kathode is applied to the tongue there is a burning sensation during the passage of the current, accompanied by a bitter taste; on opening the circuit there is a faint acido-metallic taste, which is stronger in proportion as the current had lasted longer.

According to these authors the primary taste is due to electrolysis, and the acid after-taste at the kathode is a contrast effect, comparable to the phenomena of the same order observed in the visual organs.

Certain of von Zeyneck's results (1898) also tend to show that sensations of taste produced by electrical currents are the effects of electrolytic dissociation either of the superficial fluids of the mouth or of the fluids that irrigate the cells of the taste buds. He believed, on the strength of exact electrical measurements, that on first passing a minimal ineffective current through the tongue, and then gradually increasing its potential, the anodic and kathodic sensations of taste appear with the intensity of current that produces electrolytic dissociation.

VII. It seems not improbable that there may be cases of complete congenital absence of the sense of taste, such as are known for the other special senses. A priest known to us in our native town declared that he had been unable from birth to distinguish the different flavours in his food, so that the choicest dish or the coarsest food, coffee with or without sugar, quinine or salt, wine or vinegar, were to him alike indifferent. Unfortunately, he died before we had the opportunity of testing by exact scientific methods his ability to taste (and smell), which might then have been controlled by post-mortem examination. Up to the present no clinical case has been recorded to confirm physiological inductions as to the specific nerves of taste and their

precise localisation in the peripheral taste organs. Such a case would be of the highest interest.

Partial congenital defects, on the other hand, have been frequently reported, particularly the total or partial absence of taste at the tip of the tongue. Still more common are individual variations in the localisation of sensibility to the four primitive tastes, already discussed (p. 134). Not infrequently the distinction between salt and sour is little marked, but this may possibly depend on the different use of the two terms in the language of different individuals, rather than on their dissimilar capacity of discriminating between the two tastes.

Loss of the sense of taste under morbid conditions (*ageusia*) is not uncommon owing either to peripheral lesions or to central lesions on one or both sides of part or of the whole of the gustatory area. Such paralysis may affect the power of perceiving different tastes in different degrees.

Alteration of the specific qualities of taste (*parageusia*) is fairly frequent in central diseases as the precursor of a more or less complete paralysis of taste. In a clinical case observed by Nagel unilateral paralysis of taste was preceded by a state in which the patient perceived all tastes on the affected side as *salt*.

In hysterical persons partial or total suspension of gustatory sensations is frequent. Kiesow has recently demonstrated that true hallucinations of taste may be present even in persons who are comparatively normal. Real gustatory or hallucinatory dreams have also been noted (De-Sanctis, Kiesow, and others).

The temporary, partial paralysis of taste which can be produced experimentally by the direct application of certain poisons to the gustatory organs is also of great interest. Von Anrep (1880), Knapp (1885), observed that cocaine kept for a certain time in contact with the lingual mucosa abolishes all power of taste. Aducco and U. Mosso (1866), on the contrary, found that solutions of cocaine hydrochlorate, if not too concentrated, inhibit sensibility only to bitter tastes, while for other tastes it is altered little, if at all. Oehrwall, Shore, Kiesow (1894) on repeating the experiment showed that the action of cocaine affects all qualities of taste. Oehrwall, however, recognised individual differences, and Kiesow discovered by accurate determination of liminal excitation that cocaine acts more strongly on bitter, less on sweet, still less on salt and sour taste. Shore arrived at approximately the same conclusion.

Von Anrep further showed that puncture by a needle at the edge of the tongue pencilled with cocaine caused no pain. On the other hand, Kiesow brought out the interesting fact that even strong applications of cocaine do not cause the tip of the tongue to lose its sensibility to pain and thermal stimuli. And as cocaine affects gustatory sensibility soon after its application,

and the cutaneous sensations later, he employed it to discriminate the tactile qualities of sapid substances, and thus proved that acid and salt are true gustatory sensations.

Edgeworth discovered that the masticated leaves of *Gymnema silvestre* have the property of completely abolishing the taste for sweetness. Hooper (1887) observed more accurately that sensations of sweet and bitter were entirely removed by gymnemic acid. Shore found the action of this acid to be most intense for sweet, less for bitter, still less for salt, and *nil* for acid. Kiesow confirmed these results, but found weak action even on the acid taste. He concluded that the action of cocaine is more extensive than that of gymnemic acid, and that the latter acts on sweet almost as cocaine upon bitter. According to Kiesow, gymnemic acid has no effect upon the tactile, thermal, and pain sensibility of the tongue.

Fontana (1902), under Kiesow's direction, found that eucaine-*B* has a similar action on taste to cocaine, *i.e.* predominantly upon bitter.

Ponzo found that stovaine at a certain concentration abolishes the sensations of sweetness and bitterness, while it is still possible to perceive salt and acid, though faintly. He also found that the period of anaesthesia is succeeded by a period of hyperaesthesia which is limited to certain gustatory sensations, and which he holds to be of central origin. Stovaine produces this hypergeusia for salt tastes; cocaine for sweet and bitter.

Herlitzka observed that $\frac{1}{50}$th normal solution of chromium nitrate produces hypoaesthesia for sweet and salt, and in a less degree for bitter; also that cobalt chloride causes gustatory paraesthesia for a period of 24 hours, during which all fluids taste salt.

Artificial changes of the normal mean temperature of the tongue, again, may depress or temporarily inhibit the excitability of the peripheral organs of taste. Weber first noted that on plunging the tongue for 30 to 60 minutes in water at 40° to 42° R., or into iced water for the same time, the sweetness of sugar was no longer perceptible. This observation was confirmed by Guyot, Aducco and U. Mosso, and Kiesow. Kiesow found that 10 minutes' action of iced water or warming to 40°-51° C. sufficed to make the tongue insensitive not only to sweet but also to other strong tastes, with the exception of acid, which could still be perceived under these conditions.

The temperature of the solutions employed as taste stimuli, again, affects the threshold of gustatory sensibility. According to Camerer (1880) the *optimum* of the stimulus is between 10° and 20° C. Taste sensibility, on the contrary, according to Kiesow, does not alter within the limits of temperature at which the solutions employed do not arouse decided sensations of heat or cold. Above and below these limits gustatory sensibility diminishes.

VIII. Among the most important facts in the physiology of taste is the observation that none of the four qualities, sweet, acid, salt, bitter, can be subdivided into other components. Each taste is an elementary quality that exhibits only quantitative differences; it is not possible to pass gradually from one taste to another, as in the colours of the solar spectrum and the tones of the musical scale; as yet we have no rational criterion for arranging the four tastes in a given order in series.

We have seen, in speaking of the topography of taste, that certain substances arouse different sensations according as they are applied to the tip or the base of the tongue, and that in general the sensibility to the four different primitive tastes is differently distributed over the different segments of the taste area. And we have seen the possibility of paralysing one or other of the gustatory qualities by means of specific poisons.

These facts collectively suggest, on analogy with what takes place for the different sensitive points of the skin, that the respective taste papillae differ specifically in regard to their excitability by the four primary tastes.

There is no proof of this in the histology of the peripheral organs of taste, which fails to show any difference of structure between the taste-buds of the papillae, such as it is possible up to a certain point to see in the nerve-endings for cutaneous sensibility.

It is not possible to test the individual taste-buds like the specific sensitive points of the skin. In many cutaneous regions these are far apart, while the taste-buds are grouped in large numbers in each papilla. About 400 buds lie in each of the circumvallate papillae; a lesser number in the fungiform. Each bud, moreover, represents not a single nerve-ending, but a bundle of sensory elements, so that it is not possible, as in the skin, to excite each element individually.

Still, it is interesting to excite the fungiform papillae separately, to see if each of them reacts equally to the four different tastes, or particularly or exclusively to one or two tastes alone, according as the specifically dissimilar nerve-endings conjectured are contained in each in an equal or unequal degree.

This research, which is the application to taste of the method of Blix for the skin, was undertaken successfully by Oehrwall, a pupil of Blix (1891), on the fungiform papillae of the tip of the tongue; on these it is easy to carry out a series of methodical experiments continued over several days upon the same group of papillae, previously marked and numbered, so that they can be easily recognised without any confusion. Highly concentrated solutions were employed (40 per cent sugar, 5 per cent tartaric acid, 20 per cent sodium chloride, 2 per cent hydrochloric acid), and brought into contact with the ends of the single papillae by

means of a fine brush, the point of which was smaller than the papillae. The sodium chloride solutions were soon abandoned, because the resulting sensations were not sufficiently strong and distinct. To accelerate the signalling of the sensations, the subject was forewarned of the quality of taste to be excited.

Oehrwall investigated the gustatory sensibility for sweet, bitter, and acid on 125 papillae. He began by showing that the mucous membrane between the papillae was insensitive to tastes, and further found that 27 out of the 125 papillae examined did not react to the test solutions. The 98 papillae accepted as gustatory reacted as follows:

To acid, 91.	Exclusively to acid, 12.
To sweet, 79.	Exclusively to sweet, 3.
To bitter, 71.	Exclusively to bitter, 0.
To sweet and acid, 72.	Exclusively to sweet and acid, 12.
To bitter and acid, 67.	Exclusively to bitter and acid, 7.
To sweet, bitter, and acid, 60.	

To sum up we may say that of the 98 gustatory papillae the reaction was:

To acid but not to sweet, 19.
To sweet but not to acid, 7.
To acid but not to bitter, 24.
To bitter but not to acid, 4.
To sweet but not to bitter, 15.
To bitter but not to sweet, 7.

From these results we may conclude (*a*) that not all the fungiform papillae of the apex of the tongue are gustatory; (*b*) that not all the gustatory papillae are sensitive to all the three tastes investigated; (*c*) that many (38 to 98) do not react to one or two of the tastes.

We must also bear in mind that there is another difference between the various papillae though it is more difficult to estimate it exactly; not all the papillae that are sensitive to a taste appreciate it with the same intensity; the reactions to each taste may vary in strength in the different papillae. Consequently the differences between one papilla and another are not merely qualitative but are quantitative also.

Oehrwall also experimented by the electrical stimulation of isolated fungiform papillae with a brush electrode. He found that an acid taste only appeared in the papillae which reacted to acid. He failed to arouse a sweet or bitter taste, because in order to avoid electrolytic effects he employed the induced current, with which there is a sensation of warmth and of vibration that disturbs the experiment. With the constant current Oehrwall always obtained an acid taste at the anode and a sensation of warmth in the papillae that were sensitive to acid. At the kathode he obtained a bitter or sweet taste as well as a sensation of

heat. He also found that all the papillae investigated, including the non-gustatory, were sensitive to tactile and thermal stimuli.

Goldscheider and Schmidt also tested the papillae with solutions of quinine and sugar mixed; they sometimes obtained a sweet taste only from one papilla and bitter only on another.

Kiesow's researches on the same subject were both a control and a continuation of those of Oehrwall. An important difference between the methods of the two observers is that Oehrwall's subjects were aware of the nature of the substance employed, while Kiesow kept them in ignorance. The substances used were solutions of sodium chloride (which Oehrwall gave up), sugar, hydrochloric acid, and sulphate of quinine. The hydrochloric acid was in 0·2 per cent solution, the others in almost saturated solutions.

The results practically agree with those of Oehrwall, and show that the greater part of the papillae investigated do present marked functional differences.

Of 39 papillae examined, 4 gave no reaction to any of the four substances. The other 35 (excluding doubtful reactions) gave the following results:

18 reacted to salt.	3 to salt exclusively.
26 reacted to sweet.	7 to sweet exclusively.
18 reacted to acid.	3 to acid exclusively.
13 reacted to bitter.	0 to bitter exclusively.

This table shows that of the 35 taste papillae—

9	did not react	to	sweet.
17	„	„	salt.
17	„	„	acid.
22	„	„	bitter.

This confirms the fact already brought out with another method by Kiesow and Hänig, that at the tip of the tongue sensibility is maximal to sweet and minimal to bitter, the reverse of what is observed at the base of the tongue.

Kiesow further noted the interesting fact that within the small space of a single fungiform papilla four senses may be represented—taste, touch, pain, and temperature; the sense of taste and the thermal sense can, moreover, be present in different qualities of sensation, as sweet, acid, warm, cold.

Kiesow also observed effects of peripheral fatigue which Oehrwall neglected. And lastly, he found that in dealing with these minute gustatory surfaces it was often difficult to distinguish between the salt and the acid tastes, as he had previously noted in his experiments upon children.

These results of the effects of isolated excitation of separate gustatory papillae seem to afford direct evidence that the different qualities of tastes are based on a specific differentiation of proto-

plasm in the cells of the taste-buds, or of the nerve-endings distributed to them. To explain the fact that some papillae react to a single taste, others to two, others to three, others again to all the tastes, we must admit that the qualitative differentiation of the gustatory sensibility of the epithelial cells or the nerve-endings of the taste-buds is variously developed in different papillae. The specifically dissimilar nature of the peripheral taste organs also causes their dissimilar reaction to toxic substances.

Oehrwall, on the strength of these results and of the fact that the four primary tastes are discontinuous qualities which cannot be arranged in series like musical tones of different pitch, came to the conclusion that the four tastes cannot be considered as different qualities of one sense, but are different modalities, *i.e.* four distinct senses. In the same way the sensations of heat, cold, and pressure, which were formerly considered to be different qualities of *one* form of sensibility (the tactile sense), are now recognised to be different modalities of distinct senses.

But the phenomena of *contrast* and *compensation* observed between different gustatory sensations, as between different colours, seem to contradict this theory of the plurality of gustatory senses, since they show that the tastes are intimately related to each other as different qualities of one modality of sensation.

Johannes Müller noted that after masticating the root of the aromatic calamus milk and coffee taste sour; that sweet things take away the flavour of wine, while cheese increases it. Oehrwall, however, failed to confirm the first statement; generally speaking, he found that bitter did not increase the sensibility to sweet. On the other hand, he showed that sweet did not increase the sensibility to acid, but considerably depressed it.

The observation of Aducco and U. Mosso, that when a dilute solution of sulphuric acid acts on the tongue for 5 to 10 minutes it alters the organs of taste to such an extent that distilled water is perceived as a very sweet fluid, is a more obvious contrast phenomenon. If a dilute solution of quinine sulphate is applied instead of distilled water, there is a sweet sensation at the tip of the tongue, and the bitterness is only perceived at its base and lateral edges. Solutions of formic, citric, and acetic acid do not act like sulphuric acid; hence the action of the latter is not exclusively due to its acidity.

Kiesow made a special study of contrast and showed that after excitation of the tongue with weak solutions of hydrochloric acid and salt distilled water is perceived as sweet. Laserstein saw that after the action of a 1·5 per cent solution of soda distilled water seems to be sweet. Nagel also found that on washing out the mouth with a solution of potassium chloride (which produces a faint taste of indefinite character) the gustatory

organs are altered in much the same way as by sulphuric acid, so that pure water tastes sweet.

Another interesting fact was noted by Zuntz and Heymens to the effect that a solution of sodium chloride and quinine, so weak as not to arouse any distinct taste, is still sufficient to exaggerate the taste of a solution of sugar.

There is at present no really satisfactory solution of these facts, which correspond more or less to contrast phenomena, but they do not appear to favour Oehrwall's theory, but rather to support that of a single gustatory sense. Kiesow, moreover, holds that Oehrwall's theory is contrary to direct experience, and brings out the psychological fact that the different gustatory qualities, however they may differ among themselves, have none the less something in common which distinguishes them collectively from every other category of sensation.

In defence of his theory that the four elementary tastes correspond to four distinct sense-organs, Oehrwall also questions the phenomena of compensation. He holds that on mixing two or more tastes (except when new chemical compounds arise from the mixture) it is not possible to form a new taste, and that the taste of the ingredients can always be recognised in the mixture.

Brücke expressly stated that some gustatory sensations are able to compensate each other respectively, without thereby reciprocally neutralising the stimulating substances. But the instances he adduced are not convincing, nor are they comparable with the results obtained by mixing two complementary colours which neutralise each other and yield the sensation of white. Sugar compensates or corrects the bitter taste of coffee and the acid taste of lemonade, but not in the sense of producing a new taste. Both tastes persist, and there is a mixed and more agreeable sensation. Sensations of contact, again, may obscure or modify the affective tone of a sensation, *e.g.* mustard and pepper frequently do so.

The clearest example of a compensatory effect in gustatory sensation is mentioned by Kiesow, who, on mixing weak solutions of sugar and salt in a certain ratio, obtained an insipid alkaline taste which recalled neither sugar nor salt. If more concentrated solutions are mixed the phenomenon of compensation is no longer apparent. If a mixture of two substances is taken into the mouth, one strongly sweet, the other bitter, various sensations are perceived at different times and on different spots of the tongue, some bitter and others sweet.

Kiesow saw that on combining the majority of primitive tastes in certain proportions, but always very dilute (sweet and salt, sweet and acid, sweet and bitter, salt and acid, salt and bitter, acid and bitter), they are respectively diminished in different

degrees, but it is difficult completely to abolish the two component tastes.

It is by these effects of compensation of different tastes, as well as by the varied association of gustatory with tactile, thermal, and olfactory sensations, that the flavour of nauseous medicines is corrected and the different ingredients of food materials are so combined as to convert the four primary tastes into innumerable complex flavours.

To conclude, the effects of compensation of tastes support the doctrine by which all tastes are considered as different qualities of one and the same modality of sensation.

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CHAPTER IV

THE SENSE OF SMELL

CONTENTS.—1. Peripheral organs and nerves of smell. 2. External mechanism of olfactory function. 3. Excitation of smell by odorous substances in the form of gas or of aqueous solutions. Electrical excitation of smell. 4. Chemical and physical properties of odorous substances. 5. Classification of odours. 6. Determination of olfactory acuity (olfactometry and odorimetry). 7. Specific energy of the olfactory apparatus deduced from the phenomena of partial *anosmia* and partial olfactory fatigue. 8. Corrections and compensations of odours. 9. Physiological and psychical value of olfactory sensations. Bibliography.

THE sense of smell is much less important to human life than to that of animals in general. Smell is but little developed in Man in comparison with many other animals, as appears both from the anatomical development of the olfactory bulb and the area to which the olfactory nerve is distributed, and from its functions. The olfactory apparatus of Carnivora attains such proportions that in man it is in comparison a mere rudimentary organ. The animal mind is dominated by a wealth of olfactory images, incomparably richer and more varied than those which man is capable of conceiving. It may further be assumed that the range of smells differs greatly for different kinds of animals. Herbivora distinguish useful from injurious plants by their smell; carnivora are very insensitive to the odours of plants and flowers, but have a most acute and delicate perception of animal exhalations, by which they follow the scent. The dog recognises the smell of his master, showing that different individuals exhale different odours. Hagen pointed out that different human races give off different smells. Generally speaking, it may be affirmed that the most essential needs of animal life, the satisfaction of the alimentary want and of the sex instinct, are intimately connected with the sense of smell.

Man has a narrower and less specialised range of olfactory sensation, but this does not exclude the fact that his capacity for smell, particularly for certain odours, may reach a surprising degree of sensibility. The olfactory sense seems to be more highly developed among savage races than in civilised man. Humboldt

relates that the Indians of Peru are capable of perceiving and following up the scent of game like hunting-dogs. This is probably due to the fact that they preferably use and educate their olfactory sense. Exercise, in fact, perfects the sense of smell to a remarkable extent; pharmacists are able to recognise drugs and their various properties by smell alone; experienced

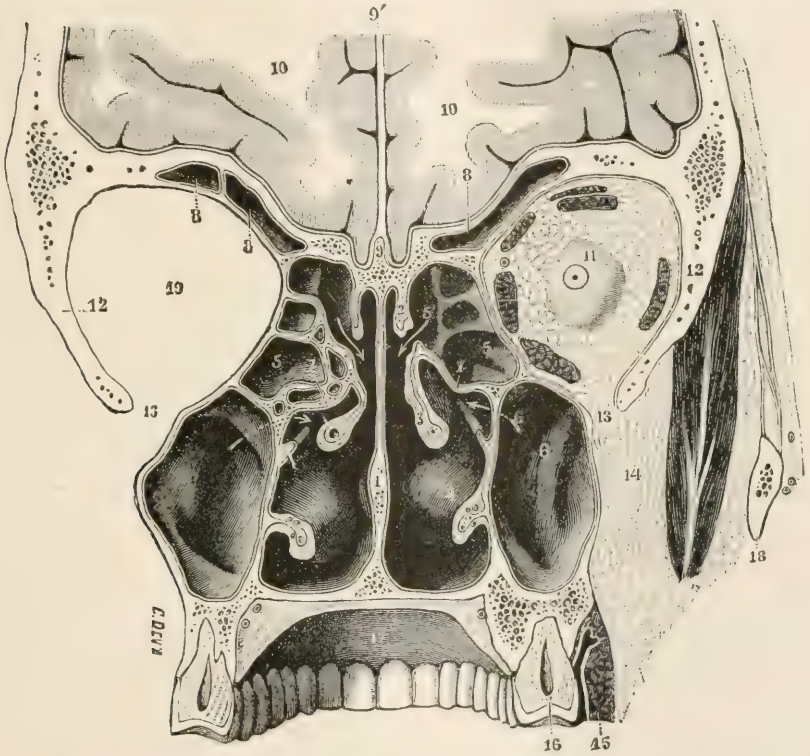


FIG. 62.—Frontal section of nasal fossae, seen from behind; the section passes through the back molars. (Testut.) 1, nasal septum; 2, upper; 3, middle; 4, lower turbinals; 5, posterior ethmoid cells opening into 5′ (to the right), superior meatus; 6, maxillary antrum opening into 6′, middle meatus; the point of the arrow is in the hiatus semi-lunaris; 7, bulla ethmoidalis; 8, frontal sinus; 9, crista galli; 9′, falx cerebri; 10, cerebral hemispheres; 11, right orbit surrounded by orbital fat, with eye-muscles; 12, great ala of sphenoid; 13, spheno-maxillary cleft; 14, adipose tissue of zygomatic fossa; 15, buccinator muscle; 16, last molar; 17, vault of palate; 18, zygoma; 19, left orbit.

physicians diagnose many eruptive diseases at once by their odour; by it wine and oil merchants know the good and bad qualities of their stock-in-trade. Wardrop tells of a man born blind and deaf who distinguished his acquaintances by their smell.

I. The specific olfactory sensory region consists of a limited portion of the mucous membrane of the nasal fossae. Seen in transverse section (Fig. 62) the nasal fossae appear as an irregular

triangle, the apex being represented by the roof, and the base by the floor of the nasal cavities. The median septum and the floor are smooth, while the lateral walls are subdivided into three irregular cavities or meatuses by the three turbinate bones. The posterior ethmoid cells open into the superior meatus, the frontal sinus, the median ethmoid cells and the maxillary antrum into the middle meatus. The functional use of these bony cavities and their communications with the mucous membrane of the nasal fossae is quite unknown.

The nasal cavities are divided into two regions: an upper, known as the olfactory region, and a lower or respiratory region. These can be distinguished by the eye, owing to their colour. In the first the mucous membrane is yellowish (locus luteus), in the

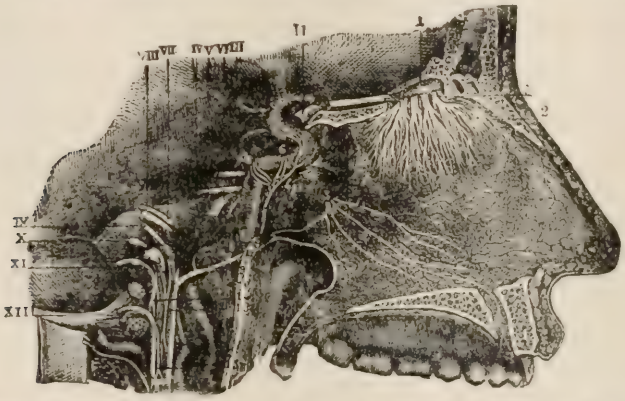


FIG. 63.—Nerves of nasal septum, seen from right side. $\frac{2}{3}$. (Sappey, from Hirschfeld and Leveille.) 1, olfactory bulb; 1, olfactory nerves passing through foramina of cribriform plate and descending to be distributed on the septum; 2, internal or septal twig of nasal branch of ophthalmic nerve; 3, naso-palatine nerves.

second reddish (Schneider's membrane). Between the median septum on the one hand and the upper and middle turbinals on the other there is only a small fissure, the sulcus olfactorius or olfactory groove. The respiratory region has a ciliated epithelium and numerous acinous glands, while the olfactory region is covered by an epithelium that has no hairs and is provided with tubular glands. Fibres of the trigeminal nerve are not only distributed all over the respiratory region of the nasal mucous membrane, but also send branches to the olfactory region.

The olfactory region is the part to which are distributed the fibres of the olfactory nerve which take origin in the bulb of the same name, traverse the pores of the cribriform plate of the ethmoid bone, form a thick plexus with narrow elongated meshes, and end in the mucous membrane of the upper third of the septum, and the pars olfactoria of the upper turbinal (Figs. 63, 64). It was formerly believed that the olfactory region also

extended over a part of the middle turbinal (Schwalbe), because the yellow portion above described is more extensive than the olfactory epithelium proper, and covers, particularly in the foetus and new-born animal, a certain portion of the middle turbinal as well. But the work of Max Schultze and the measurements of von Brunn showed that the region innervated by the olfactory nerve is confined in adults to a portion of the upper turbinal and of the septum. Von Brunn carried out his investigations on two adult subjects, aged from thirty to forty. He made sections of the nasal mucous membrane, and was thus able to determine the true extension of the olfactory epithelium. In the first subject the

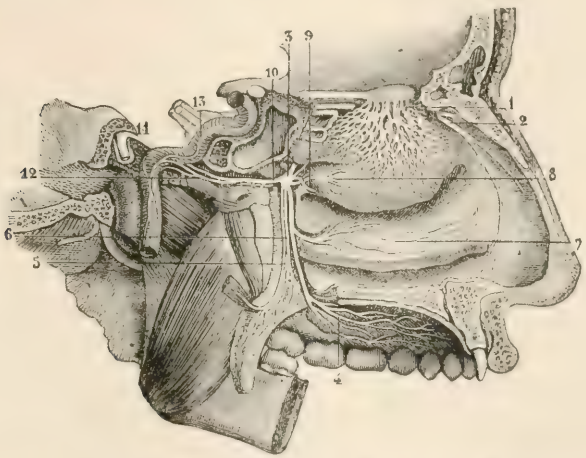


FIG. 64.—Nerves of outer wall of nasal cavity. ½. (Sappey, from Hirschfeld and Leveillé.) 1, network of branches of olfactory nerve descending into the region of the upper and middle turbinals; 2, external branch of nasal nerve; 3, spheno-palatine ganglion; 4, ramifications of great palatine nerve; 5, small palatine nerve; 6, external palatine nerve; 7, branch to region of lower turbinal; 8, branch to region of upper and middle turbinals; 9, naso-palatine branch to septum (divided).

olfactory region of the right side measured 238 sq. mm., in the second 257 sq. mm. So that the dimensions of this area are comparatively restricted, as it only amounts to about 5 sq. cm. for both nostrils.

In the olfactory region two different kinds of epithelial cells were described by Eckhardt in the frog (1855), and by Ecker in man and in certain mammals (1856). M. Schultze (1863) distinguished them as olfactory cells and columnar epithelial cells. The former are true peripheral nerve cells, which are directly continuous with the fibres of the olfactory nerve; the second are merely special supporting cells (Fig. 65). This distinction, which Exner at first disputed, was subsequently confirmed by the Golgi method.

The peripheral end of each olfactory cell is continued into a

small process, surmounted, according to von Brunn, by a bunch of short, fine hairs (Fig. 66). With Golgi's method it is possible to follow the varicose fibres of the olfactory cells to their dendritic ramifications in the so-called glomeruli of the olfactory bulb, and to determine their relations with the fibres of the olfactory tract (Fig. 67).

That the olfactory nerve is exclusively the nerve of smell is a physiological theory that has only slowly gained ground, and even to-day there are many who hold no decisive opinion. Galen's





FIG. 65.—(Left.) Cells of the olfactory region. Highly magnified. (M. Schultze.) 1, from the frog; 2, from man; *a*, epithelial cell, extending into a long ramified process; *b*, olfactory cells; *c*, their peripheral processes; *e*, their extremities, seen in 1 to be prolonged into fine hairs; *d*, their central filaments.

FIG. 66.—(Right.) An olfactory cell, human. (v. Brunn.) *n*, central process prolonged as an olfactory nerve-fibril; *b*, body of cell with nucleus; *p*, peripheral process passing towards the surface; *c*, knob-like termination of peripheral process; *h*, bunch of olfactory hairs.

view that the olfactory sense has its seat in the cerebral ventricles, and that odorous particles reach it through the foramina of the cribriform plate, was first questioned at the end of the eighth century, when the Greek monk Theophilus Protospatarius recognised the olfactory nerve as the organ of smell, by means of which the odorous vapours are carried to the brain during inspiration, and the superfluous moisture is given off in expiration.

As evidence that the olfactory nerves are the specific nerves of smell Schneider adduced an observation by the Bolognese anatomist, Eustachio Rudio, who in 1600 claimed to have known a youth

who was destitute from birth of any sense of smell, and in whom the post-mortem examination revealed absence of the olfactory nerves. Diemerbrök and Mery attributed the capacity of perceiving smell to the nasal branches of the fifth nerve as well, but without convincing the majority of physiologists, by whom the function is attributed wholly to the olfactory surface.

Bellingeri (1818) and Cloquet (1828) supported this view. Magendie, on the contrary, sought by numerous publications (1824–41) to revive the earlier view of Diemerbrök and Mery, and stated that no positive proof was forthcoming to show that

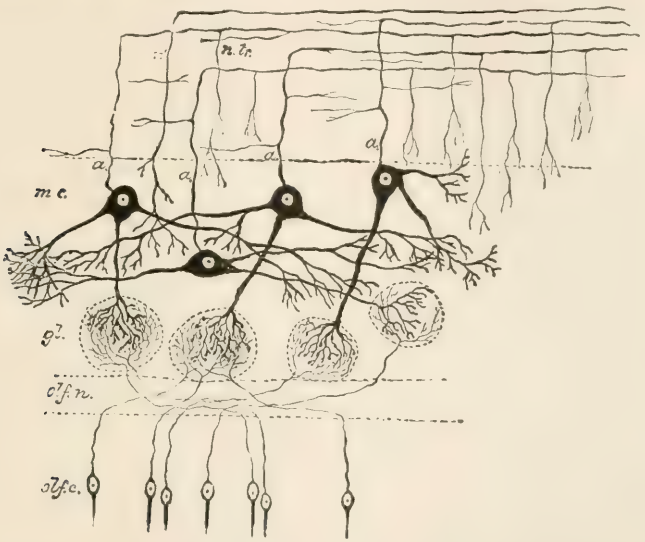


FIG. 67.—Diagram of the connection of cells and fibres in the olfactory bulb. (E. A. Schäfer.) *olf. c.*, cells of the olfactory mucous membrane; *olf. n.*, deepest layer of the bulb composed of the olfactory nerve-fibres, which are prolonged from the olfactory cells; *gl.*, olfactory glomeruli, containing arborisations of the olfactory nerve-fibres and of the dendrons of the mitral cells; *m. c.*, mitral cells; *a*, their axis-cylinder processes passing towards the nerve-fibre layer, *n. tr.*, of the bulb to become continuous with fibres of the olfactory tract; these axis-cylinder processes are seen to give off collaterals, some of which pass again into the deeper layers of the bulb; *n'*, a nerve-fibre from the olfactory tract ramifying in the grey matter of the bulb.

the other nerves to the nasal mucosa (sensory branches of the trigeminus) did not participate in the function of smell. But he evidently interpreted as effects of olfactory sensation the reflex acts that can be excited in dogs deprived of the olfactory nerves, by means of irritating vapours capable of acting on the tactile and sensory nerves of the nasal mucous membrane. This was demonstrated by Eschricht, Bell, Bishop, Joh. Müller, Dugés, and Picht. The two last observers, who had no true olfactory sensibility, were susceptible to the excitation due to the vapours of acetic acid, ammonia, and the like, which provoked sneezing. Bidder, Wagner, Longet, Vulpian, pronounced against Magendie's opinion;

Malherbe, Giannuzzi, and Claude Bernard in favour of it (Bernard on the strength of a dubious clinical case). The experimental results and clinical observations of Valentin, Schiff, and Prévost in our opinion leave no room for doubt that the olfactory nerve is the exclusive nerve of smell.

II. The specific olfactory surface is well protected by its remote position against pathological processes as well as inadequate stimuli; on the other hand, it is easily accessible to adequate stimuli, *i.e.* to such as can arouse olfactory sensations, save when a nasal catarrh or any other circumstance closes the olfactory groove.

Odorous substances may reach the nasal cavities and the olfactory surface in two ways: by the nostrils, penetrating with the air introduced during inspiration, and by the choanae, with the air expelled during expiration. In both cases it is necessary in order to produce a perception of smell that the air-current shall reach the olfactory surface. When an odorous substance is brought under the nose, there is no sensation of smell, even when the nostrils are open, so long as the breath is held or breathing performed through the mouth.

Even in ordinary quiet respiration the olfactory sensations are not always very plain, particularly with weak-smelling substances. To obtain clear sensations, it is necessary to breathe deeply, or better to make rapid, short, and repeated inspirations by sniffing. It is doubtful whether this act is accompanied by active dilatation of the nostrils (Bidder, Fick, Valentin) or whether they are not more or less tightly closed (Bell, Diday, Funke, Braune, Clasen, von Vintschgau, and others). Diday, to bring out the importance of constriction of the nostrils in sniffing, observes that after forced dilatation by the introduction of a glass tube into the nose, almost every olfactory sensation ceases on breathing in an odoriferous substance.

Apart from this purely secondary question these facts show that in ordinary respiration air that penetrates the nostrils does not enter by the olfactory groove, while in sniffing some at least of the air does reach that region.

A. Fick showed by a very simple experiment that the anterior portion of the nostril is more important in the function of smell than the posterior. When a rubber tube connected at the other end with a vessel containing an odorous substance is introduced into the nose, no smell, or at most a very slight odour, is perceived, if the mouth of the tube is directed towards the middle or lower turbinal. If, on the contrary, it is turned towards the roof of the nasal fossa, in the direction of the olfactory groove, a perceptible sensation of smell is obtained. If the posterior portion of the nasal aperture is stopped olfactory acuity remains intact; if, on the contrary, the anterior part is blocked the sense is considerably weakened.

This explains the interesting observation of Béclard, that persons who have lost the projecting portion of the nose by disease or injury have no sense of smell. In such cases the air passes directly through the choanae, without ascending to the olfactory region.

In order to determine the path by which the air-current normally passes through the nasal cavities, Paulsen (1882) in Exner's laboratory performed an interesting experiment on the head of a human corpse. He sawed through the cranium in the middle line to expose the nasal fossae, and then applied small pieces of red litmus paper to different regions of the nasal mucous membrane at short distances from each other; after this he reunited the two halves of the skull. He then set up artificial respiration through a bellows of approximately the same capacity as the lungs, which he attached to the trachea, and passed air containing ammonia vapour through the nostrils, when the litmus paper turned blue in the parts of the mucous membrane over which the ammonia passed.

The results of these experiments were quite clear. The reaction of the litmus paper showed that the inspiratory air-current describes a curve in the nasal cavity, first passing upward, and then turning towards the choanae. Moreover, the air which penetrates through the anterior portion of the nostril rises higher than that which enters by the posterior portion.

On reversing the direction of the current, *i.e.* when the air charged with vapour is driven from the choanae to the nostril, the result was quite different; the curve described by the current of air follows a somewhat lower level than in the previous experiment. Zwaardemaker, Franke, and more recently Danziger and Rethi, essentially confirmed the results of Paulsen, although they varied his method in different ways. Zwaardemaker used the plaster cast from one-half of the nasal cavity of a horse in which the septum had been replaced by a glass plate. A glass tube was inserted into the posterior part, and the soot of a petrol lamp placed in front of it blown through by means of an aspirator. This could be followed by the eye, and it was seen that the region innervated by the olfactory nerve remained free from soot. Franke sawed through a human skull in the middle line, stained the whole of the mucous membrane black, replaced the nasal septum with glass, and blew white tobacco smoke through the nostrils by a bellows, which showed up well through the glass partition on the black ground. This experiment, like the preceding, showed that in ordinary quiet breathing the air inspired through the nostrils did not reach the olfactory region, but described a curve over the middle meatus, and middle and upper part of the septum.

The observations made by Kayser on the living subject also

agree with the above. He caused a fine magnesia powder to be aspirated, and then, with the rhinoscope, investigated the parts of the mucous membrane to which it specially adhered.

Since then it is proved that the inspiratory current as such does not reach the olfactory region, it is clear that the odorous molecules cannot be carried thither by the stream of air, but must reach it by some other means. We know from Bloch's work that the temperature inside the nose is above 30°, so that Zwaardemaker's hypothesis that odours penetrate to the sensory end-organs of smell by a process of gaseous diffusion remains the most probable. The act of sniffing which draws the air-current higher into the nasal cavities must undoubtedly facilitate the diffusion and penetration of odours into the olfactory region.

Bidder assumed that smells can only be perceived during inspiration, and denied that they can be carried to the olfactory region during expiration as well. But Paulsen's experiments showed that the expiratory current takes the same curved path as the inspiratory, only running somewhat lower, which may impede, but cannot hinder, the diffusion of odours in the olfactory region. On the other hand, it is easy to show that odorous substances breathed in through the mouth and breathed out through the nose may give rise to distinct olfactory sensations. That these are weaker than those excited by inspiration through the nose is sufficiently explained by the fact that the odorous substances inhaled through the mouth must pass through all the air-passages, where they may be partially absorbed before being brought into contact by the expired air with the olfactory region. Again, during mastication of solid food and particularly during the deglutition of alimentary boluses and of fluid, the vapours and odoriferous particles exhaled by the foods and beverages may on passing through the choanae above the soft palate reach and excite the olfactory surface during expiration. This fact is important, because it establishes the intimate relations and associations between the senses of taste and smell which we discussed in the last chapter. The mechanism by which the olfactory sense is excited during a meal depends principally on the fact that at each act of swallowing the soft palate is suddenly raised, on which the air saturated with odorous exhalations is driven from the choanae towards the olfactory region at a pressure, according to Fick, of about 30 cm. water. When deglutition is completed, there is a deeper expiration than usual, and the air of the pharynx charged with the odours exhaled by the food is driven through the choanae. The olfactory sensations thus aroused can, as Chevreul showed, be easily eliminated if the nostrils are kept closed with the finger.

Nagel rightly pointed out that the appreciation of smell through the choanae is of higher biological importance, particularly

for man, than that which takes place through the nostrils. Man, in fact, does not snuff up his food while he eats it, like the animals that have an elongated nasal aperture placed near the buccal orifice. Man uses the sense of smell (in combination with taste) much more during mastication and deglutition than during the act of putting the food into his mouth.

The popular theory that smell is the sentinel of the respiratory apparatus, as taste is of the digestive apparatus, cannot be accepted unreservedly in the light of physiological experience. We are protected from breathing noxious air by the nasal branches of the trigeminal, and not by the olfactory nerve. Irritating gases, even when they are capable of arousing olfactory sensations, are specially perceived by the sensory branches of the nasal mucosa. The chief importance of smell is, in association with taste, to perceive the quality of foods, to influence their selection, to excite appetite, and reflexly to promote the digestive secretions. The suppression of smell is dangerous to man because it disturbs all these functions, and not because he becomes incapable of enjoying the perfume of flowers or the aphrodisiac exhalations of certain secretions.

III. As in the sense of taste, the adequate stimuli for smell are chemical in their nature, and the odoriferous substances must come into direct contact with the olfactory surface before the olfactory end-organs can be excited. The earlier opinion that odours may act at a distance upon the olfactory organ, by special aerial or ethereal undulations, as do sound and light, is now wholly abandoned, and has no foundation. The fact, as pointed out by Longet, that odours can be carried by the wind to a distance of several miles, in itself, according to Zwaardemaker, proves the corpuscular theory of smell, and excludes the possibility that they can be due merely to vibrations.

The number of substances capable of exciting smell, that is of giving out odours, is certainly very great, and many bodies that seem to us to have no smell are odorous for certain animals; this is due to the limited development of our sensibility. Even if all the substances that are volatile, or dissociable into the finest particles, are not odoriferous, at any rate for man, it may still be said that the most penetrating and characteristic odours we know are given off by volatile substances.

Certain other substances that are normally non-volatile and inodorous give off odours under certain conditions. Arsenic, *e.g.*, which at an ordinary temperature has no smell, gives off a strong smell of garlic on heating; resin and many metals become odorous under friction. Accordingly, it is often held that both under ordinary conditions and under special physical influences an atmosphere of minute particles emanates from the surface of many bodies, and that these may be perceived by their scent, if not by

man, at any rate by other animals, when they reach the olfactory area of the nasal mucous membrane along with the inspired air.

Tourtual (1827) stated that odours are only perceptible in the gaseous state. E. H. Weber (1847) gave support to this view by a number of experiments. He bent his head so far back that the nostrils were directed upwards, and then injected water into the nasal fossae so that the olfactory region should be as full as possible. He found that when the water had run out, the function of smell was lost for 30 seconds, and then returned gradually, but did not become normal again for 2½ minutes. A solution of sugar had the same effect as pure water. The injection of water scented with eau de cologne produced a smell at the first moment of injection; but all olfactory sensation disappeared when the nasal cavity became full; on emptying it smell was abolished for a time, as on injecting pure water. Valentin (1848) confirmed Weber's results, and found that on emptying the nose of the injected water the tactile nerves of the nasal mucosa recover their activity before the olfactory nerves. Fröhlich (1851) obtained much the same results.

The loss of olfactory sensibility thus produced depends, according to Weber, on the saturation of the olfactory epithelial cells of Schneider's membrane with water, which checks their function. But it is more correct to suppose that the injection of plain water, particularly at a low temperature, alters the epithelium of the nasal mucous membrane, and causes a nasal catarrh which is sufficient of itself to produce diminution or total inhibition of olfactory activity.

According to Aronsohn (1886), Weber's theory that odours are imperceptible in a watery solution is erroneous. On Kronecker's suggestion he substituted a solution of physiological saline for the pure water douche, adding an odoriferous substance and raising the temperature to 38° C. He used 0·5 c.c. oil of cloves in 250 parts of saline at 38°, and was able to smell it, on filling the nasal cavities by a nasal douche apparatus, for 30-40 seconds. Temperatures above the normal (38°-44° C.) are more favourable than lower temperatures, perhaps because they increase the excitability of the olfactory nerves.

Aronsohn also experimented with camphor, eau de cologne, cumarine, and vanilla. The degree of dilution of these odours required to evoke a definite sensation, and also the concentration required for solutions to reach the threshold of excitation, vary. The indifferent (isotonic) solution of sodium chloride is 0·7-0·75 per cent, preferably 0·73 per cent, which corresponds with the fact discovered by Rumsberg that the tissue fluids contain 0·62-0.73 per cent sodium chloride.

Sodium chloride may be replaced by other salts, each of which has an optimum degree of concentration which is indifferent to

the excitability of the olfactory cells. If the osmometric equivalent (*i.e.* that which carries odours) of sodium chloride = 1, then that of sodium carbonate = 2, that of sodium sulphate = 4, that of sodium and magnesium phosphate = 6.

The most important fact discovered by Aronsohn is that these salt solutions which have been regarded as odourless have each their own more or less definite smell. Vaschide came to the same conclusion.

Nagel, Haycraft, and Zwaardemaker all disputed Aronsohn's statements. Zwaardemaker objected that it is impossible to expel the air completely from the upper part of the nasal cavity by Aronsohn's method. If any bubble of air is left the odorous substance will be exhaled into it, and may excite the olfactory surface in the form of gas. According to Zwaardemaker the question must remain undecided till experiments on the dead subject have proved the possibility of completely filling the nasal cavity.

Veress set out to solve the problem on these lines. Before experimenting on the living body he made careful studies on anatomical subjects, using the right nostril of a human head sawn through in the middle line. In this way he was able to make direct observations on the path of the fluid introduced into the nose, and further sought to determine which position of the body was most favourable to complete filling of the nose, and what amount of fluid was necessary. He obtained good results from a posture at an angle of more than 35°. In his experiments on the living subject he tilted the head to postures of 50° to 80°. He also tried to reproduce possible pathologico-anatomical modifications, such as displacement and thickening of the middle turbinal, variations in the olfactory groove, etc. He pointed out that errors may arise also from the mucus that covers the walls of the nasal cavity, since this may contain bubbles of air that are not removed until the mucus itself has been expelled: and he imitated the mucus in his preparations with a thick solution of gum.

After these preliminary studies on the dead body, Veress set to work on the living subject. He discovered an error in Aronsohn's method, owing to the fact that the dorsum of the nose formed the lowest part of the nasal cavity. Veress, on the other hand, by bending the upper part of the body forward, obtained a position of the head in which the olfactory surface really lies lowest. Although in certain positions 1 c.c. of fluid is sufficient to cover the olfactory area, he used so much that the excess ran out of the nostrils. He also examined the effect of an indifferent solution of sodium chloride at body temperature upon the olfactory end-organs, by first filling the nose with it, and then replacing this by a similar solution containing the odorous substance to be investigated. Veress attributes great importance to the influence of temperature,

which is eliminated by his method. The substances examined were: eau de cologne, ylang-ylang, essbouquet, oil of cloves, oil of origanum, oil of peppermint, camphor-water, caproic acid, and caproic acid with addition of piperidine.

Veress found that even when pain was avoided by careful filling of the nasal cavity, sodium chloride specifically excited both the olfactory end-organs and the endings of the trigeminal nerve, and further pointed out that the sensibility of the olfactory area to this fluid is altered after a strong bath. Veress speaks of symptoms similar to those that occur in coryza, which in his opinion come under the category of olfactory and gustatory sensations.

As to the effect of the odoriferous substance contained in the saline, Veress says that when the two fluids are completely mixed there is a compound sensation which cannot be accurately defined, in the production of which both the respiratory and the olfactory areas participate. In this compound sensation, according to Veress, the tactile sensations predominate, and the gustatory sensation is weak. That the olfactory area proper is really concerned in it can be controlled by the fact that its sensibility is diminished after a bath. If, for instance, when all the fluid had been removed from the nasal cavity the subject was still able to perceive the odour, Veress considered the experiment a failure, since it was doubtful whether the olfactory groove had been entirely filled. For this reason he questions Vaschide's results, because no appreciable diminution of olfactory sensibility appeared in his experiments.

After much practice Veress succeeded in distinguishing some odorous substances from others, and divided them into different groups. Thus, for instance, it was difficult to distinguish eau de cologne from ylang-ylang, camphor from oil of peppermint, oil of cloves from oil of origanum, while it was easy to say if the exciting substance were oil of cloves or ylang-ylang, camphor or oil of origanum, oil of peppermint or caproic acid. But he pointed out that it was to some degree possible to identify the group to which any substance belonged, by means of its action on the mucous membrane. He compared this ability to recognise the odorous substances with that by which a man born blind recognises through his tactile sensations certain qualities of external sensations which a normal individual is incapable of knowing by touch, and further claims that associative processes may take part in this act of recognition. Veress came to the general conclusion that an odoriferous substance brought into contact with the olfactory organ in the form of fluid may be regarded merely as a heterologous stimulus for that organ.

Veress observes that we cannot speak of an olfactory sensation in aquatic animals in the sense in which we use it of mammals:

he refers to the work of Nagel, and contends that the experiments made by Aronsohn on fishes are not above criticism. Aronsohn offered to fishes ants' eggs dipped in clove oil or tincture of asafoetida, and saw that they retreated from the food, even if still several millimetres away from it. From this he argued that the olfactory organs were excited, but Veress thought it equally probable that the retreat was due to excitation of the tactile organs.

Notwithstanding these elaborate researches, we are hardly justified in asserting that all classes of fishes are entirely unprovided with the sense of smell, especially as the olfactory organs are so highly developed. If it were so we should have to assume that the olfactory cells of fishes have functions other than those in air-breathing animals.

Further, it is evident, as pointed out by Johannes Müller, that the essential part of an olfactory sensation lies not in the gaseous nature of the odorous substance, but in the specific sensibility of the olfactory organs, and in their differentiation from all other sense-organs.

On the other hand, there are direct observations, the earliest of which date back to Aristotle, that tend to show that fishes possess a sense of smell which is specifically distinct from all other sensations. Milne Edwards points out that sharks often come from afar to devour the carcases thrown into the sea, and that other fishes of the same class show distaste for food that gives off odours. Other authors, on the contrary, including Nagel, agree with Veress in denying that fishes and aquatic amphibia have any sense of smell comparable with that of terrestrial animals.

The question seems to us to be decided by the experiments of v. Uexküll on Selachians (1894). He took certain specimens of *Scyllium* that had been deprived of food for some time, and extirpated the olfactory mucous membrane of the nasal fossae in some, leaving it intact in others. He found a difference in the behaviour of those which had and had not been operated on. The latter, shortly after food had been placed in their tank, either loose or in a bag, became very restless and began to swim in search of it. According to v. Uexküll washing the hands in the tank after touching sardines was enough to throw the intact fishes into a state of excitement. Those operated on, on the contrary, seemed quite unaware of the presence of food, even when it was placed close to them.

These experiments seem to establish the existence of a sense of smell at least in Selachians. Other experiments by v. Uexküll show it to be quite distinct from the sense of taste, as he found that normal dogfish will take a sardine covered with quinine sulphate into their mouths, but immediately reject it. Consequently, it is not taste but smell which guides them in seeking

their food; and they reject the unappetising morsel, not by smell but by taste.

Accordingly, even if Aronsohn's experiments on man were carried out by an imperfect method, the conclusion he arrived at, that the olfactory sense can be excited by odorous substances dissolved in fluid, agrees well with what is known for fishes.

Very few researches have been made on the olfactory organ with *inadequate* stimuli. Among these the electrical current alone has given some positive, even if doubtful, results. Volta failed to observe any effect of an olfactory character; Ritter obtained a special sensation similar to that aroused on looking at the sun or sniffing up tobacco (excitation of tactile and pain sense). He subsequently noted near the kathode the sensation felt before sneezing, and occasionally a trace of ammoniacal odour: at the anode, on the contrary, there was sometimes a sensation of acid which may have been due to spread of current to the taste-buds. More interesting results were obtained by Althaus from a patient affected with bilateral paralysis of the trigeminal nerve. On applying strong galvanic currents to the Schneiderian membrane he obtained a smell of phosphorus.

Aronsohn made a number of investigations by his method, passing a current through the nasal fossae filled with an isotonic solution of sodium chloride at 38°. Different olfactory sensations were aroused according as the anode or the kathode was applied. The kathodic smell occurred during the closure of the circuit, the anodic at the opening. The kathodic smell was regularly stronger than the anodic. The quality of the two sensations, which approximate to the gustatory impressions, was indescribable. When an odoriferous substance in solution was employed, its characteristic smell was altered by the electrical current.

According to Valentin it is possible by mechanical stimulation of the nostrils to produce unpleasant olfactory sensations which last for some time. But other observers failed to obtain any results.

Thermal stimuli arouse no olfactory sensations, even when the nasal fossae are filled with fluid at 0° or at 50° C.

IV. At present we know little of the chemical and physical properties which a substance must have in order to be an adequate stimulus of the olfactory end-organs. We are wholly ignorant of the correlation between the physico-chemical constitution of a body and the quality and intensity of the odours it is capable of arousing. Some substances that differ greatly in chemical constitution have much the same odour; on the other hand, some substances that are chemically allied have a very different smell.

Haycraft (1888), Passy (1892), and Zwaardemaker (1895) brought out some interesting facts in relation to this intricate subject. In the periodic system of Mendeléeff and Lothar Meyer

the elements that form odoriferous compounds belong almost exclusively to the fifth, sixth, and seventh groups.

The fifth group contains nitrogen, phosphorus, vanadium, arsenic, niobium, antimony, didymium, tantalum, bismuth. The sixth group consists of oxygen, sulphur, chromium, selenium, molybdium, tellurium, wulfranium, uranium. The seventh group consists of fluorine, chlorine, manganese, bromine, iodine. It is undeniable that many of these elements form odoriferous compounds, and that a certain periodicity in the appearance of odorous and non-odorous substances exists within each series.

Another interesting fact is that in some series of homologous chemical compounds, *e.g.* in those of the fatty acids and the alcohols, there is a regular and continuous change in the odour. It is particularly remarkable that the lowest members of these homologous series have very faint smells, and that the intensity of the smell continuously increases in higher members (formic, acetic, propionic, butyric, valerianic, caproic acid, etc.). In the highest members the series of odours is interrupted; stearic acid, *e.g.*, has no smell. Another series of regularly changing smells consists of benzol, toluol, xylol, etc.

Undue importance was given in the past to the so-called odoroscopic researches of B. Prévost (1799) on the physical quality of odours. He observed that many odoriferous substances assume a characteristic rotary or vortex movement on the surface of water, which he interpreted as the effect of the discharge and diffusion of odorous particles into the atmosphere. Liégeois brought forward other odoroscopic phenomena, but expressly noted that they only appeared in substances of vegetable and animal origin, while those of mineral origin show no movement on contact with water (*e.g.* ammonia, hydrogen sulphate and phosphate). On the other hand, he found that some completely inodorous substances, such as sulphuric acid, potash, and soda, exhibit the same phenomenon. Obviously these "odoroscopic phenomena" afford no explanation why odorous substances excite the organ of smell: the movements are due to the surface tensions of the different compounds, and are not a specific property of odours.

Tyndall also showed that the vapours of odorous substances possess a remarkable power of absorbing thermal rays, but it is very doubtful if it is owing to this property that they are odorous.

Erdmann's researches on the solubility of certain essential oils (cedar, rose, geranium) in liquid air are extremely interesting. In comparison with other chemical compounds, these odorous substances have a very high specific solubility in liquid and possibly also in gaseous air. It is probable that this property is common to all odorous substances and that it is one of the

conditions in virtue of which they are able to excite the olfactory end-organs.

V. The qualities of odours are extraordinarily numerous. No one, as Nagel justly points out, can say that they know all the substances capable of exciting specifically distinct sensations of smell; many people are not acquainted with certain very characteristic odours familiar to chemists, *e.g.* formaldehyde, picric acid. We cannot as a rule recognise the components in a mixture of many odours. It is also possible to make a gradual transition from one to another of two very different odours by a series of mixtures, in which the two components are present in different proportions. In this respect smell differs very markedly from taste, in which, as we have seen, there are few specifically distinct qualities of sensation, so that the components are easily recognised in any mixture.

Granting all this, it is not surprising that we have as yet no true scientific classification and scale of odours. We are not even able to distinguish the different qualities of odours by different names, and to express them we employ the names of the vegetable or animal substances from which they emanate. Lastly, we cannot differentiate odours into elementary and compound.

It has, however, been attempted by different methods to classify odours in certain groups or categories. Haller proposes to arrange them in three groups, according as they are pleasant, unpleasant, or indifferent: *odores suaveolentes*, *odores intermediae*, *odores foetores*. The first class includes particularly the ethers and essential oils: among the foul smells are certain gases of very simple composition (sulphuretted hydrogen, carbon bisulphide, certain hydrogen carbides, etc.), as well as certain decomposition products (indole, skatole, etc.). But it is impossible to distinguish the two classes sharply from one another and to determine the odours belonging to the intermediate class, because these distinctions are based exclusively on subjective appreciations which vary considerably in different individuals. Moreover, some gases, *e.g.* chlorine, bromine, iodine, ammonia, which have a bad smell when concentrated, are, on the contrary, indifferent or even pleasant when suitably diluted.

At first sight the classifications of odours proposed by Fröhlich seems better. As the nasal mucous membrane is supplied by two pairs of nerves, the olfactory and the nasal branches of the trigeminal, the first of which alone is the specific nerve of smell, while the second serves touch, temperature, and pain, the sensations generated here must also be placed in two categories, *i.e.* those resulting solely from excitation of the olfactory nerve, and those which are due to excitation of other sensations as well. The former are *pure olfactory sensations*, *e.g.* those produced by ethereal oils, resins, balsams, etc., which never give rise to reflex

movements; the latter owe their origin not merely to stimulation of the olfactory nerve but also to that of the nasal branches of the trigeminal, as by chlorine, iodine, bromine, nitric acid, ammonia, oil of mustard, rape, etc., which always produce reflex movements. But if the fact is more closely investigated, it is seen that very few odorous substances excite pure olfactory sensations. Nearly all, when they act with a certain intensity, affect not only the olfactory sensibility but also the general sensibility of the nasal mucous membrane. Thus, oil of juniper and of bergamot and even camphor, which Fröhlich considered to be purely olfactory substances, irritate not only the nasal mucosa but the conjunctiva of the eye as well.

In order to give some notion of the innumerable qualitative varieties of odours the classification of (purely olfactory) odorous substances into nine groups proposed by Zwaardemaker may be reproduced :—

I. Class : *Odori eterei* (Lorry)—
- (*a*) Essences of fruits used in perfumery (apple, pine-apple, pear, etc.).
- (*b*) Beeswax.
- (*c*) Ethers, aldehydes, ketones.

II. Class : *Odori aromatici* (Linnaeus)—
- (*a*) Camphoric odours (camphor, borneol, patchouli, rosemary, eucalyptus, turpentine).
- (*b*) Odours of drugs (clove, ginger, pepper).
- (*c*) Odours of anise and lavender (menthol, oil of fennel, arnica, thymol, chamomile).
- (*d*) Odours of lemon and of rose (palisander, sandal-wood, cedar-wood, etc.).
- (*e*) Odour of bitter almond (hydrocyanic acid, benzoic and salicylic aldehyde, nitro-benzol).

III. Class : *Odori balsamici* (Linnaeus)—
- (*a*) Odours of flowers (jessamine, syringa, lilies of the valley, orange-blossom, acacia, etc.).
- (*b*) Liliaceous odours (iris, narcissus, hyacinth, violet, mignonette).
- (*c*) Vanilla odours (benzoin, balsam of Peru and Tolu storax, cumarine, heliotrope).

IV. Class : *Odori ambrosiaci* (Linnaeus)—
- (*a*) Odours of amber.
- (*b*) Odours of musk (nitro butyltoluol, ox-bile, many animals, some fungi).

V. Class : *Odori agliacei* (Linnaeus)—
- (*a*) Sulphuretted hydrogen, hydrogen carbide, vulcanised rubber, asafoetida, gum ammoniacum, ichthyol.
- (*b*) Arsenuretted hydrogen, phosphoretted hydrogen, trimethylamine.
- (*c*) Chlorine, bromine, iodine, quinine.

VI. Class : *Odori empireumatici* (Haller)—
- (*a*) Odour of roast coffee, toasted bread, tobacco smoke, pyrocatechin, guiacol, creosol, acrolein, piridine.
- (*b*) Odour of amylic alcohol and homologues, benzol, toluol, xylol, phenol, creolin, naphthalin, naphthol.

VII. Class : *Odori caprilici* (Linnaeus)—
- (*a*) Caproic acid and homologues, cheese, sweat, putrefying bones, rancid fat.
- (*b*) Cat's urine, vaginal secretion, spermatic fluid, chestnut flour.

VIII. Class: *Odori repugnanti* (Linnaeus)—
(*a*) Narcotic odours of *Solanaceae*, henbane, etc.
(*b*) Odour of bugs, of ozoena.
IX. Class: *Odori nauseanti* (Linnaeus)—
(*a*) Odour of carrion.
(*b*) Faecal odour (scatole).

VI. Delicacy of smell, or the power of perceiving slight differences in the intensity of odours, is often distinguished from olfactory acuity, or the capacity of distinguishing minimal amounts of odorous substances. But the two expressions may be used indifferently, because acuity practically coincides with delicacy of smell.

Olfactory acuity differs very much for different odours; it is measured by determining their liminal values. To find the liminal value Valentin (1855) placed small quantities of odoriferous substances in a large glass vessel of known capacity, and approximately determined the minimal quantity required to render the air contained in the flask capable of stimulating the olfactory end-organs; or he mixed the odoriferous fluids with large amounts of water, and then tested by smell the minimal dose of odorous substance that could be appreciated. By these methods he found, *e.g.*, that the minimal perceptible amount of essence of roses is 1/200,000 mgrm., of tincture of musk 1/2,000,000 mgrm.

Fischer and Penzoldt (1887), and Passy (1892), made further experiments on the olfactory acuity to different odours, and perfected the methods employed by Valentin. Passy dissolved the substances in alcohol, and from the stock solutions made very weak dilutions, of which he poured a small drop into an empty litre flask, and then tested by sniffing at the mouth of the flask whether the odour were perceptible. All experimental errors in this research tend to raise the threshold of excitation. The following figures, however, give some idea of the extraordinary delicacy of smell for certain odours:—

	mgrm.	per litre of air.
Essence of orange	0.00005	0.001
Essence of wintergreen	0.000005	0.0004
Rosemary	0.00005	0.0008
Ether	0.0005	0.004
Camphor	5	0.005
Heliotrope	0.1	0.05
Cumine	0.05	0.01
Vanilline	0.05	0.0005
Natural musk	0.01	0.00005
Artificial musk (trinitrobutyltoluol)	0.00001	0.000005

Fischer and Penzoldt made an interesting experiment on the olfactory acuity of man. They tried to determine the minimal perceptible amount of mercaptan in the air of one of the rooms

in the laboratory. They found that 1 23,000,000 mgrm. of this substance diffused in a litre of air gave a feeble but quite distinct olfactory sensation. When we reflect on this extraordinary sensitiveness in the rudimentary human olfactory organ, we can obtain some idea of the enormous olfactory acuity of certain animals in which the olfactory mucous membrane is not limited to the nasal cavity but extends as far as the frontal and sphenoid sinuses.

We owe to Zwaardemaker the invention of a practical method which facilitates quantitative research into the acuity of smell. He gave the name of *olfactometry* to the investigation of olfactory sensibility for odours in general, and of *odorimetry* to the measurement of the comparative sensitiveness to different specific odours.



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FIG. 68.—Indiarubber olfactometer connected with a Marey's tambour. (Zwaardemaker.) Consists of the olfactometer tube, which runs inside a tube of vulcanised rubber. By pulling this out more or less a different extent of the odoriferous surface is exposed. The tambour records the moment at which inspiration begins. It is connected with a branch of the olfactometer tube by a small receiver which holds pure water, to prevent the smell of the rubber tube of the recording apparatus from affecting the subject. In ordinary examinations of olfactory acuity the recording apparatus is not used.

As early as 1888 he invented a very simple apparatus, the *olfactometer*, which consists of a graduated glass tube (10 cm. long, 5 mm. wide—internal diameter) which runs easily inside a second tube coated on the inner side with some solid odoriferous substance, *e.g.* vulcanised rubber (Fig. 68). The curved end of the glass tube is introduced into one of the nostrils. If the outer tube is entirely covered by the inner glass tube, no smell is perceived on sniffing through the latter; but if the glass tube is drawn out so that a greater or less surface covered by the odorous substance is exposed, an odour is perceived on sniffing through the olfactometer; its intensity increases with the area of the surface exposed.

Zwaardemaker proposes as the unit of qualitative measurement the sensation obtained when the rubber cylinder is exposed for

a length of 1 cm.; he found that this stimulus is on an average the *minimum perceptible* stimulus of the olfactory organ under physiological conditions, and called this unit an *olfactie*. But on testing the olfactory acuity of a number of individuals by the olfactometer, it is found that they vary considerably even under apparently normal conditions.

In odorimetric investigations, by which it is sought to establish the olfactory qualities of different substances, Zwaardemaker replaced the rubber cylinder by cylinders of porous clay previously steeped in solutions of the odoriferous substances (Fig. 69). The liminal value of 1 cm. length of tube of course varies for each substance, as this figure is merely the unit of minimal stimulus, or olfactie, for the smell of india-rubber.

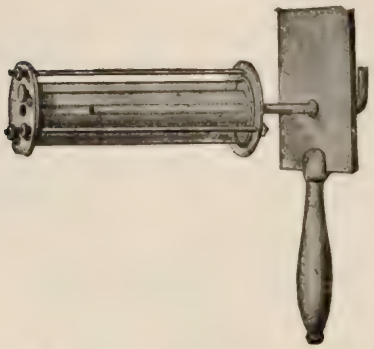


FIG. 69. Olfactometer with porous clay cylinder which can be saturated by various odoriferous fluids. (Zwaardemaker.) The glass olfactometric tube runs inside the porous tube, which is contained within a wider glass tube. The test solution is introduced by a pipette through a small hole (afterwards closed by a screw tap) into the space between the glass tube and the outer surface of the porous tube. The curved end of the olfactometer tube is passed into one nostril. The wooden screen prevents the odoriferous substance from penetrating to the other nostril.

VII. The problem whether smell, like the other senses, is represented centrally by a number of specific energies is peculiarly difficult, because we are not yet able to make any systematic classification of the infinite number of odours, nor to distinguish elementary from compound odours, as we can in the case of taste. But even if it is impossible under existing scientific conditions to enumerate the specific energies comprised in the range of olfactory sensations, this does not exclude us from assuming generally that a certain number of specific energies must exist at the olfactory centres to enable us to perceive or recognise the quality of odours.

Some interesting facts can be adduced in support of this view, and may now be briefly recapitulated. In the first place we must draw attention to the cases of *partial anosmia, congenital or acquired*. Some normal individuals, while possessing a well-developed sense of smell, are unable to perceive special odours.

Blumenbach states that many people cannot perceive the scent of mignonette, while their sense of smell is perfect for all other odours. Joh. Müller recognised this partial defect of olfactory sensibility in himself. To him the scent of mignonette was merely a grassy smell. Cloquet, Mackenzie, and Reuter noted cases of anosmia limited to the vanilla group. It is recorded that other normal individuals could not smell violets. Generally

speaking, cases of partial congenital anosmia are rare; but it may be doubted whether they are so in reality, or whether the absence of smell for certain odours has not been overlooked or left undiagnosed, and only discovered accidentally. The English chemist D. H. Nagel was unable to perceive the specific odour of cyanic acid, which resembles that of bitter almonds, and found the same in several of his students, though their smell was normal for all other odours.

Cases of partial anosmia after illness are more frequent. Zwaardemaker draws attention to the alterations of smell after diphtheria and influenza; in certain cases, which he investigated, the anosmia does not extend to all odours. Sensibility to certain smells appears to be abolished, to others it is merely weakened, to others unchanged. Winkler in his neurological clinic observed a tabetic who exhibited almost complete anosmia for the smell of benzoin, though he recognised the smell of musk. In the same clinic another patient could not smell musk, but perceived benzoin better than other odours.

Parosmia and *subjective* or *hallucinatory smells* also have a certain importance in regard to the question of the specific olfactory energies.

Joh. Müller describes a patient who constantly complained of bad smells, and the post-mortem examination showed that the arachnoid had ossified in several places, and there were areas of softening in the cerebral hemispheres. A. Dubois knew a man who after a fall from his horse had for many years till his death the sensation of a foetid odour. Many physicians have observed patients who had a constant sensation of a smell of burning, similar to that produced by lighting wooden matches. Other patients complain of a persistent smell of faecal odours. It is important to note that these hallucinatory sensations are perceived most distinctly during the inspiratory act and on sniffing, as if the activity of the perceptive centre was aroused by the olfactory substances introduced with the air to the peripheral organ. We may exclude Ludwig's suggestion that the subjective sensation of faecal odours in some patients depends on reabsorption into the blood of the products of intestinal putrefaction, which directly excite the olfactory centre. Zwaardemaker proved, in fact, that olfactory hallucinations may be associated with complete objective anosmia to the odours perceived subjectively.

Generally speaking, olfactory hallucinations are rare. Smell is seldom represented in dreams (Brillat-Savarin, De Sanctis, Kiesow and others), although the two last believe it is more common than is generally supposed. This agrees with the fact that it is difficult, even by a strong effort of will, to evoke memory images of the commonest smells, as we can easily recall visual, and particularly acoustic and musical, sensations. But that in certain cases

olfactory memory images can be called up is amply proved by the researches of Kiesow on the so-called spontaneous representations. Not all the sensations of which patients, particularly hysterics, complain can be regarded as hallucinatory, merely because they are not perceived by normal individuals. In many cases they depend on a *hyperosmia* or abnormal lowering of the threshold of olfactory sensibility, in consequence of which odours not normally perceptible can be detected. But there was undoubted hallucination in the case of a hysterical woman who was aware of an unpleasant taste of menstrual blood some time before the commencement of menstruation.

The partial temporary anosmia that can be artificially produced if the olfactory apparatus is fatigued by prolonged exposure to different strongly odoriferous substances is of great importance in the classification of odours.

We know that smell is easily fatigued by long-continued exposure to odorous substances. Anatomists who are in the dissecting room for long periods finally cease to notice the cadaveric odours; patients with foetid wounds or suppurations cease to smell the foetor that disgusts their nurses; those who cure furs or work in drains become accustomed to repugnant smells, and fail to perceive them.

Aronsohn showed that very strong odours depress the activity of the olfactory apparatus in a few minutes, and that after exhaustion a certain time, at least 1-3 min., is necessary to restore excitability. On sniffing tincture of iodine the smell was appreciated only for 4 minutes, balsam of copaiba for 3-4 min., camphor 5-7 min., ammonium sulphate 4-5 min., turpentine 5 min.

Zwaardemaker obtained more exact results with his olfactometer. He constructed curves of progressive fatigue of the olfactory organ, when excited by odorous substances of constant intensity over a regularly increasing number of seconds. The measure of fatigue is indicated by the progressive rise of the threshold of excitation, *i.e.* the minimal stimulus perceptible after repeated stimulations of increasing duration. Fig. 70 shows four curves of olfactory fatigue, two obtained with rubber (at a strength of 10 and 14 olfacties), and two others with benzoin (intensity 3·5 and 9 olfacties). The first glance shows that the threshold rises, owing to fatigue of the olfactory sense, with the duration of excitation, and the more rapidly according to the strength of the stimulus. On comparing the two curves obtained with rubber and the two with benzoin, it is seen that the latter causes fatigue far more rapidly than the former, although the intensity of the stimulus was less.

This olfactory fatigue or exhaustion observed after sniffing odorous substances for a certain time does not extend to all

odours, but generally assumes the more or less definite characters of partial anosmia.

A methodical study of this interesting subject might show the best way to solve the problem of the classification of odours according to their specific energies. But the results so far obtained have not corresponded with these expectations.

Among the experimental researches in this direction, those of Fröhlich and of Aronsohn promised important results. Both

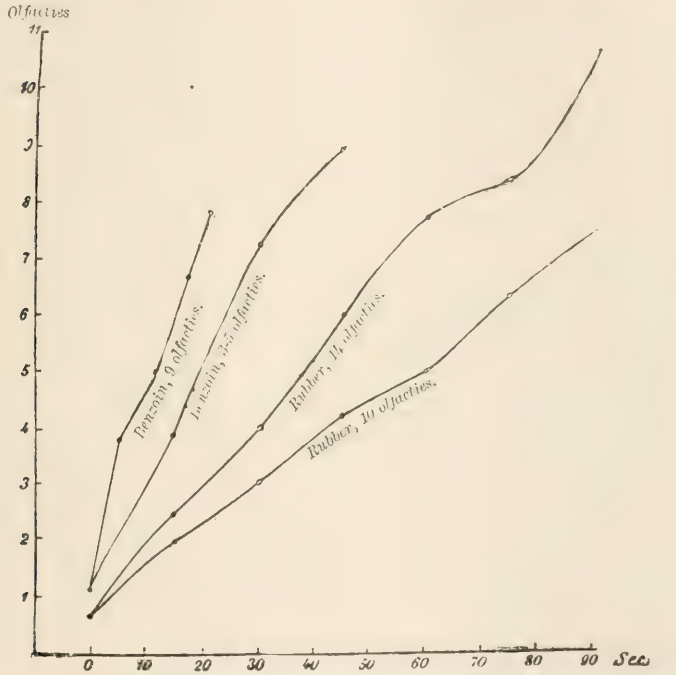


FIG. 70.—Curve of olfactory fatigue. (Zwaardemaker.) The liminal values are marked in olfacties on the ordinates; the duration of stimulation in seconds on the abscissæ. The four curves (two of caoutchouc of 10 and 14 olfacties; two of benzoin of 3.5, and 9 olfacties) show a more or less marked rise in the liminal value after successive stimulations of increasing duration. The length of the olfactory stimulations is regulated by a metronome which marks seconds. The subject takes a deep breath every two seconds.

fatigued their sense of smell by a special odour, and then sought to determine the odours for which olfactory sensibility was still normal, or had been diminished to the same extent as for the odour experimented with. Theoretically, different specific energies must be assumed for the first, and identical energies for the second.

Fröhlich's researches led to no unequivocal practical conclusions; Aronsohn's, on the contrary, while carried out by a less exact method (he took no account of the intensity of the different odours) led to some results that deserve mention. He found that

after fatigue by tincture of iodine he was able to distinguish ether and ethereal oils naturally, and oil of cedar, turpentine, bergamot, and cloves somewhat less distinctly; his smell was, on the contrary, considerably blunted for alcohol and copaiba balsam. After fatigue by copaiba balsam he was able to distinguish ethereal oils, ether, and camphor. On the other hand, after losing his sensibility to camphor, he could no longer smell eau de cologne, oil of cloves, or ether. The results of fatigue by ammonium sulphide were more surprising: sensibility remained perfect, or almost so, for ethereal oils and cumarine, but was absolutely lost for sulphuretted hydrogen, hydrochloric acid (7 drops in 50 of water), and bromine (1 in 1000). Aronsohn concluded from this that ammonium sulphide, sulphuretted hydrogen, and the halogens form a single class of odours with the same specific energy. He concluded that different qualities of odours affect different parts of the olfactory nerve.

Zwaardemaker and Nagel carried out similar experiments. If two odorous substances that do not affect each other chemically, *e.g.* cumarine and vanilline, in aqueous solution, are mixed in such proportions that the scent of vanilla alone is perceptible, then, after exhausting the sensibility of the olfactory organ to the latter, the odour of cumarine alone remains perceptible on sniffing the mixture. This result leads to the conclusion that different specific energies underlie the two odours named, although in Zwaardemaker's classification they belong to the same class, even to the same subdivision of odours.

Attempts to support the theory of a number of specific olfactory energies have been made from the effects of certain local or general poisons. Fröhlich found that on sniffing at 5 grms. morphia mixed with sugar, smell was perceptibly blunted. If 1 cgrm. strychnine and sugar is held in contact with the Schneiderian membrane for 20 minutes a profuse secretion of mucus is produced, which lasts eight days; there is a simultaneous exaggeration of olfactory acuity. Internal use of strychnine also produces hyperosmia. The internal administration of atropine and daturine, on the contrary, inhibits the power of differentiating between odours for several hours.

Experiments on the partial anaesthetising of the olfactory mucous membrane by cocaine are also interesting. The first observations of this kind date from the year 1888 (Lennox Browne, Gremt). Kiesow (1894) observed that if the nasal mucous membrane is painted high up with cocaine, olfactory sensibility decreases very much, and entirely disappears to certain smells. Goldzweig obtained similar results. Zwaardemaker, however, made the first systematic investigation on the toxic action of cocaine. He found that sensibility was unaltered to some odours and weakened to others, but the results did not conform with his classification. He further observed that the

state of anosmia was preceded by a brief period of hyperosmia. Reuter made a very interesting communication to the effect that the anosmia produced by the action of cocaine is not only preceded but also followed by a period of hyperosmia, as the effect of the cocaine is wearing off. Rollet then observed that on return to the normal state after the action of cocaine there is a period in which the liminal value oscillates considerably.

Rollet further experimented with gymnemic acid and produced a long period of total anosmia, after which he found that the appreciation of single qualities of smell returned at unequal intervals.

From these observations as a whole it must be assumed that the olfactory apparatus contains a certain number of component elements (which are probably more numerous than those of taste) endowed with specific sensibility to different elementary qualities of smell. But in the present state of our knowledge this difficult subject is far from being cleared up.

VIII. In daily life, as in medicine and pharmacology, bad smells are often corrected by other more pleasant odours. In perfumery it is a common practice to mix different scents in order to obtain pleasant olfactory sensations. To form a clear picture of the effects of mixing different odours, or of their simultaneous action on the two halves of the olfactory mucous membrane, it is necessary to distinguish several possible cases.

Sometimes on mixing odoriferous gases or vapours with other gases new inodorous compounds are formed. Thus ammonia and acetic acid form ammonium acetate, which has no smell. According to Nagel an inodorous compound is also formed when the smell of formaldehyde is counteracted by ammonia. Clearly in these cases there is no physiological neutralisation of two olfactory sensations.

Again, the sensation produced by an unpleasant odour may be succeeded by a stronger and more penetrating smell. In this case the stronger smell alone excites our olfactory sense, but the weaker does not disappear. It no longer excites the sense of smell, either because its liminal value has been displaced, or because attention is concentrated on the stronger odour. The use of perfumes is generally directed to the disguising of bad smells. Preparations of creolin or hypochloride of lime are used to disguise the smell and disinfect the purlieus of public conveniences. Tar corrects the odour of ozoena, carbolic acid of gangrene. Castor oil and cod-liver oil, which have for many people an unbearable smell and taste, are made less unpleasant by the addition of various substances.

When two equally strong odours act separately on the two nasal fossae, it is possible to perceive the one or the other odour alternately.

Valentin experienced this on smelling ether and balsam of Peru at the same time. He concluded that there was a conflict between the two olfactory sensations analogous to that observed in the two visual fields, according as attention is fixed on one or other of them. The same olfactory conflict was noted by Aronsohn between the smell of camphor and that of cedar oil.

In other cases there is no such conflict on stimulating the olfactory sense by two odours at the same time, nor does the

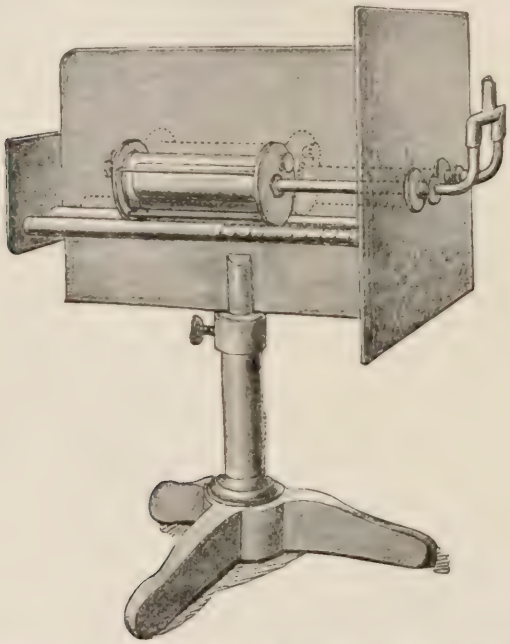


FIG. 71.—Zwaardemaker's double olfactometer with porous tubes. Its construction is the same as that of the simple olfactometer (Fig. 69). The two olfactometers are separated by metal diaphragms, and run on two rods marked in centimetres. The ends of the olfactometer tubes are introduced into the two nostrils, when two different odours are simultaneously employed. Or they may be united by the T-tube shown in the figure, so as to stimulate only one nostril simultaneously with both odours.

stronger smell predominate; but there is a more or less perfect neutralisation, and the two odours become fainter or disappear entirely. Thus Aronsohn saw that the smell of camphor disappeared on simultaneously smelling petrol, eau de cologne, essence of juniper, or garlic, though all these odours are weaker than that of camphor.

Zwaardemaker made a scientific study of these neutralisation effects. For this purpose he employed his *double olfactometer* (Fig. 71). With this instrument he was able to apply a different odour of measurable intensity to each nasal fossa by introducing

one nozzle of the olfactometer into each nostril, or both odours could be made to act on one nostril alone by uniting the two olfactometers by a T-junction.

The liminal value, or minimal perceptible intensity of each of the odours to be experimented with, is first determined. This estimation has to be made for each nostril separately, since it is rare to find both equally sensitive. The minimal amount of each odour perceptible to each nasal fossa is the *olfactie*, and corresponds to a certain length (measured in centimetres) of exposure of the olfactometer tube. When this has been determined it is easy to vary the intensity of the olfactory stimuli in measurable quantities (of 1, 2, 3 . . . olfacties), and to change the relative intensity of the two odours in the two olfactometers.

By this method Zwaardemaker established that full compensation is obtained when the nostrils are separately stimulated with the following pairs of odorous substances in the proportions indicated as follows:—

	In centimetres of the olfactometer.	In olfacties.
Cedar wood and rubber	5·5 : 10	2·5 : 14
Benzoin and rubber	3·5 : 10	3·5 : 10
Paraffin and rubber	8·5 : 10	8·5 : 14
Rubber and wax	10 : 7	14 : 28
Rubber and balsam of Tolu	10 : 7	14 : 70
Wax and balsam of Tolu	10 : 9	40 : 90
Paraffin and wax	10 : 5	10 : 20

If the relative intensity of any pair of these substances is altered, either the strongest smell alone is perceived, or there is a conflict between the two sensations, or only a very weak and indefinite sensation, or lastly, a disappearance of all sensation when there is perfect neutralisation. According to Zwaardemaker there is never, even with very strong odours, a *mixed sensation*, *i.e.* a psychical combination of the two olfactory sensations, tending to a reinforcement or sensible qualitative alteration in the perception of one or the other odorous substance.

One of the most interesting experiments that can be made with Zwaardemaker's double olfactometer consists in filling the one with acetic acid (2 per cent), the other with ammonia (1 per cent). On leading the two odorous substances separately to the two nostrils, a smell of ammonia or of acetic acid is obtained, according as the one or other cylinder is the more exposed. The two smells are never simultaneously perceptible. It is, however, possible to find such a relation of intensity that neither of the two odours prevails over the other, or there is at most a weak smell of one or the other. Lastly, it is possible to discover such proportions that on sniffing with the two nostrils no olfactory sensation results, even when the two stimuli are so strong that either, separately, would arouse an intense sensation.

If this surprising phenomenon, discovered by Zwaardemaker, took place in the open air, it could easily be explained as the effect of the chemical combination of the two odours, which would form ammonium acetate. But this explanation will not hold for the double olfactometer, because the two substances are separated during the entire period of excitation by the nasal septum. It is therefore a physiological effect, analogous to, but more complete than, the compensations of gustatory sensations studied by Kiesow.

Zwaardemaker's assertion that the simultaneous excitation of smell by two or more different odours never elicits a *compound* or *mixed* sensation was contradicted by later researches of Nagel, who came to the following conclusions:

(*a*) It is possible for any two odours to fuse into a mixed sensation, which, at least for a few seconds, gives the impression of a simple odour of a new quality.

(*b*) The mixed odour is a persistent or transitory sensation, according as the fatiguability of the olfactory organ is approximately equal or different for the component odours.

(*c*) If instead of only two, a large number of substances are mixed, as by perfume makers, it is easier to obtain a more persistent and decided mixed odour.

(*d*) The mixed odour may resemble the component odours without being identical with them; in other words, it is always a qualitatively new sensation.

Zwaardemaker took up this question again, and admitted the existence of *true mixed odours*, but declared that they only appear when the component odours are very nearly allied, *i.e.* when they belong to the same or to an allied class. When, on the other hand, two odours of different and dissimilar classes are brought together, there is not a mixed odour, but a neutralisation or conflict between the two sensations—neutralisation if the stimuli are weak, conflict if they are strong. Moreover, there are certain variations in the strength of the stimuli, within which the effects of compensation or of struggle do not disappear. To produce a conflict the stimuli need not necessarily be equal in intensity, or of the same value in olfacties. When weak stimuli are used the intensity can only be varied within narrow limits; but there is a wider range of variation when stronger stimuli are employed.

To this Nagel replied that compound or mixed odours may be formed by mixing odours not only with similar but also with dissimilar substances. He obtained unmistakable mixed smells with vanilline and bromine, amyl acetate and iodine, turpentine and xylol, etc. It is true that owing to the different volatile properties of the odorous substances, and to the unequal fatiguability of the olfactory organ to different stimuli, the

sensation of a mixed odour readily breaks up into its components, and the phenomenon of conflict sets in; but theoretically it is important that a sensation of new quality can, even temporarily, be produced on mingling different and very dissimilar olfactory stimuli. According to Nagel, this phenomenon presents a certain analogy to what is observed for colours.

IX. As regards the physiological value of olfactory sensations, it should be noted that they not infrequently excite reflex acts, in the motor system and in that of the glands, which may be useful alike to the individual and to the species.

We have elsewhere seen that Pawlow noted a profuse salivary and gastric secretion in the dog when the animal had merely sniffed at its food. We also pointed out the special importance to the coming together and pairing of the sexes in many mammals of the venereal odours that emanate from the mucous glands of the sex-organs. Olfactory excitations undoubtedly play no inconsiderable part in the sexual life of man.

The repugnant smells that emanate from putrefying foodstuffs, from excreta, and from certain poisonous substances induce instinctive acts directed to the rejection of these substances for food, or to removing or concealing them. At the same time it must be noted that not all foul smells come from noxious matters, nor do all noxious matters give off bad smells.

There are close relations between the olfactory sensations and the sphere of emotion. All odours that reflexly excite the activities of vegetative and reproductive life constantly produce a feeling of pleasure. But numbers of other olfactory sensations are associated with a feeling of pleasure or distaste, without connoting any physiological value or significance. These have none the less a more or less definite psychical value. Smell is perhaps more capable than any other modality of sensation of profoundly altering that general affective state of the mind which we call mood. Where there is a bad smell, one becomes impatient and irritable; in a pleasantly scented atmosphere the tone of the mind alters, and we become cheerful or gay.

Another characteristic of olfactory sensations is their capacity of calling up by imagination the memory images of distant places, objects or events with great clearness. Nagel notes that the smell of tar calls up a seaport, the acrid smell of machine oil revives the memory of a sea-voyage.

In conclusion it is found that certain special olfactory sensations sharpen the wits, and aid the processes of ideation and judgment. The use and abuse of tobacco to which literary persons are especially prone is partly justified by these psychically stimulating effects.

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CHAPTER V

THE SENSE OF HEARING

CONTENTS.—1. The organ of hearing. 2. Functions of the external ear. 3. Functions of the tympanic apparatus (tympanic membrane and chain of ossicles). 4. Functions of internal ear muscles (tensor tympani and stapedius). 5. Functions of tympanic cavity, Eustachian tube and fenestra rotunda (cochleae). 6. Structure of organ of Corti, and dissimilar vibratory properties of the rods, basilar membrane, and tectorial membrane. 7. Compound tones, noises, simple tones, and differences of pitch and strength. 8. Limits of the perceptive capacity for tones, and faculty of discriminating between different tones. 9. *Timbre* or quality of simple and compound tones. 10. Acoustic phenomena perceived on the simultaneous production of several tones. 11. Theory of perception of simple and compound tones. 12. Consonance and dissonance of tones, musical chords. 13. Rising and falling phases of auditory sensation; auditory fatigue. Entotic and subjective auditory sensations and hallucinations. 14. Binaural audition and localisation of sounds. Bibliography.

WE have already seen that from both the morphological and the physiological point of view the Internal Ear has two distinct portions, one of which is innervated by the vestibular, the other by the cochlear branch of the eighth cerebral nerve, and that they represent two distinct sense-organs (see Vol. III. p. 405).

The peripheral organ of hearing is the Labyrinth (cochlea) with the terminations of the cochlear nerve, to which alone the name of *auditory nerve* should be applied. The Vestibular organs (saccule, utricle, and semicircular canals) may, as we have seen, be extirpated in birds and mammals without causing any perceptible depreciation of hearing; the destruction of the cochlea, on the contrary, produces deafness.

The vestibular organs—which regulate the tone of the muscles reflexly by means of sub-conscious impulses (p. 111)—are phylogenetically a stage in evolution from primitive cutaneous sensibility; the cochlear organ, which subserves auditory sensations, represents a much later stage in evolution—it is absent in fishes, first appears in amphibia and reptiles, increases in birds, and finds its maximal perfection in mammals.

The adequate stimulus of auditory sensations consists in the vibrations of elastic bodies, within certain limits of frequency and intensity. These vibrations are transmitted through the air to

the organ of hearing, and penetrate to and stimulate the endings of the auditory nerve, and arouse the sensations of tones and noises in the sensory centres.

I. Of the three parts into which the organ of hearing is divided (Fig. 72) the internal ear alone contains in the cochlea the terminal sense-organ that is excited by sound vibrations; the outer and middle ear are mere complementary physical parts of the apparatus, which serve to promote and facilitate the conduction of sound-waves to the cochlea.

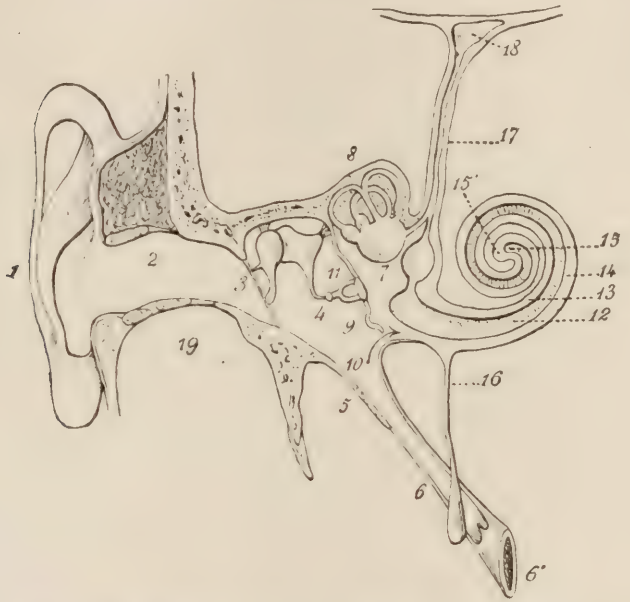


FIG. 72.—Diagram of the human ear as a whole. (After Debierre.) 1, pinna or auricle; 2, external auditory meatus; 3, tympanic membrane; 4, stapes attached to fenestra ovalis (vestibuli); 5, bony portion of Eustachian tube; 6, cartilaginous portion; 6', its internal orifice; 7, cavity of vestibule filled with perilymph; 8, semicircular canals with utricle; 9, promontory; 10, fenestra rotunda (cochleae) with arrow indicating tympanic orifice of cochlea; 11, tympanic cavity filled with air; 12, cochlear canal filled with endolymph, united to sacculus vestibuli by small canal; 13, scala vestibula; 14, scala tympani terminating in fenestra rotunda; 15, apex of cochlear canal, where the two scalae unite at 15'; 16, cochlear aqueduct; 17, vestibular aqueduct; 18, endolymphatic sac; 19, parotid region.

The external ear consists of the pinna, and the external auditory canal or meatus, closed at the end by the tympanic membrane.

The middle ear, or tympanic cavity, is an irregular, hollow chamber with bony walls, filled with air. It contains the chain of auditory ossicles—the malleus, incus, and stapes, with their two short muscles—the internal aperture of the Eustachian tube which opens into the pharynx, the fenestra ovalis (vestibuli) closed by a membrane, to which the base of the stapes is inserted,

and the free fenestra rotunda (cochleae), closed by a membrane known as the secondary membrane of the tympanum, which is directly connected with the scala tympani of the cochlea.

The internal ear or labyrinth contains in two distinct parts the sensory end-organs innervated by the two branches of the

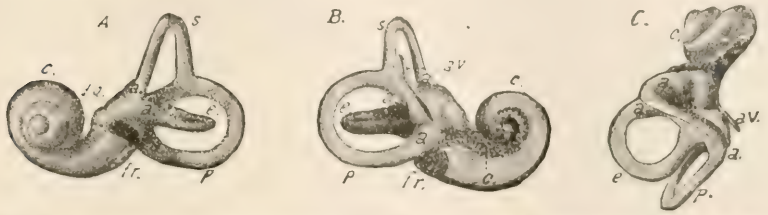


Fig. 73.—Cast of the interior of the labyrinth. Left human ear. ⅔. (From Henle.) *A*, seen from outer side; *B*, from inner side; *C*, from above; *s.*, superior; *p.*, posterior; *e*, external or lateral semicircular canals; *a.*, their ampullae; *a.c.*, aqueduct of the vestibule; *f.o.*, fenestra ovalis (vestibuli); *f.r.*, fenestra rotunda (cochleae); *c.*, spiral tube of cochlea.

eighth nerve: the utricle, saccule, and the three semicircular canals with their respective ampullae innervated by the vestibular nerve, and the cochlea, innervated by the cochlear nerve. The osseous labyrinth (Fig. 73), hollowed out of the petrous bone, must

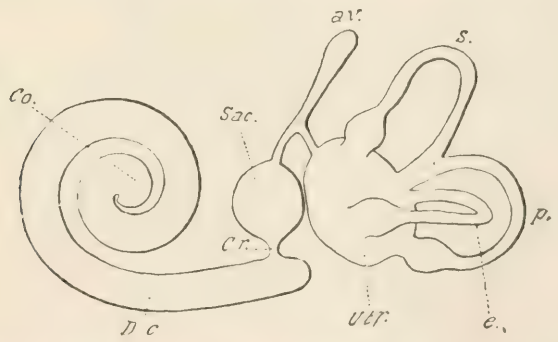


Fig. 74.—Left membranous labyrinth, viewed externally. (Merkel.) *Co.*, cochlea; *Dc.*, ductus cochlearis; *Sac.*, saccule; *Utr.*, utricle; *s.*, *e.*, *p.*, superior, external, and posterior semicircular canals; *a.c.*, aquaeductus vestibuli; *C.r.*, canalis reuniens.

be distinguished from the membranous labyrinth (Fig. 74), which lies within it. The space between the two is filled with perilymph, while the interior of the membranous labyrinth contains the endolymph.

The cochlea is the acoustic portion of the labyrinth; it consists of a spiral tube, divided into two chambers by a bony septum (lamina spiralis) completed by a membranous portion (membrana spiralis). The lower chamber or scala tympani communicates by the fenestra rotunda with the tympanum; the upper chamber,

the scala vestibuli, opens into the vestibule. At the apex of the cochlea the two communicate by a small opening (helicotrema).

Between the two scalae is a smaller canal, triangular in section, the scala media, or ductus cochlearis (canal of the cochlea), which is bounded by the slender membrane of Reissner facing the scala vestibuli, and the spiral or basilar membrane facing the

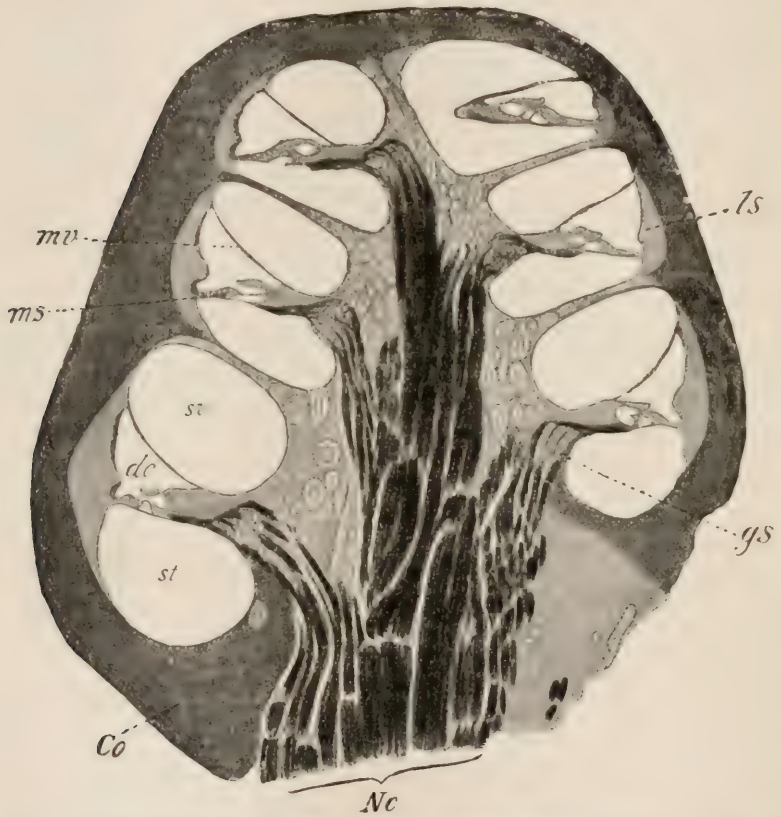


FIG. 75. -Section through cochlea of the cat. Magnified 25 diameters. (Sobotta.) *d.c.*, duct of cochlea; *g.s.*, ganglion spirale; *Co.*, bony wall of cochlea; *l.s.*, ligamentum spirale; *m.s.*, membrana spiralis or basilaris, supporting organ of Corti; *m.v.*, membrana vestibularis or Reissner's membrane; *N.c.*, nervus cochlearis; *s.v.*, scala vestibuli; *s.t.*, scala tympani.

scala tympani. This canal contains the endolymph of the membranous labyrinth of the cochlea, and within it and just above the basilar membrane is the very delicate organ of Corti, the terminal apparatus of the cochlear nerve. As shown by Fig. 75 the cochlear nerve penetrates the central canal of the modiolus, and sends its branches along the osseous spiral lamina to the basilar membrane and the organ of Corti.

This brief review of its elements will elucidate the study of the complex peripheral apparatus of audition. We shall study the morphological details more closely later on, in discussing each portion of this apparatus, with the object of bringing out its physiological importance.

It is easy to show by experiment that the outer and middle ear of man are not of fundamental importance to hearing. If the external auditory passages are stopped, hearing is undoubtedly diminished more to the deeper than to the higher tones of the musical scale, when transmitted through the air. Both, however, can be distinctly perceived through the bones if the sounding body, *i.e.* a vibrating tuning-fork, is applied to the skull (mastoid apophysis, forehead, etc.).

The transmission of sounds and tones occurs normally through the bones when we listen to our own voice. The vibration of the vocal cords throws the bones of the skull into vibration and thus excites the organ of Corti independently of air-transmission through the outer and middle ear. It is an everyday observation that after stopping the auditory meati our own voice sounds much louder. Again, when the head is dipped into water sounds are transmitted through the skull, because the sound-waves of water behave like the sound-waves of solid bodies.

That the external and middle ear are physical instruments for the improvement of hearing is shown by the fact that the sound-waves of the air are communicated with great difficulty to solid and fluid bodies. That is why on stopping our ears it is very difficult to understand any one speaking in ordinary tones. Apart from the difficulty in the transmission of air-vibrations to the bones of the skull, Rinne has shown that hearing is more sensitive when excited through the tympanum than it is when excited through the bones. When the vibrations of a tuning-fork held between the teeth have become so feeble that the ear no longer distinguishes them, they become audible again if the tuning-fork is brought near the external ear.

When the transmission of sound-waves through the ordinary air-passages becomes impossible owing to disease of the outer and middle ear, there is relatively a very pronounced deafness.

If the cochlear labyrinth remains sound, this deafness can to some extent be remedied by means of Rhodes' *audiphone*, which consists of a broad, thin plate, which is brought into connection with the teeth, and thus gathers up the sound-waves from the air, and transmits them to the organs of Corti.

II. In man the auricle or pinna is an organ of complicated form, but in other mammals it generally takes the shape of a more or less elongated trumpet, usually directed upwards, less often downwards. In the human pinna we must distinguish the helix (which occasionally presents Darwin's tubercle), antihelix,

tragus, antitragus, lobule, and the concha which surrounds the entrance to the meatus. The muscles which move the pinna as a whole are the retractor, adductor, and elevator, while those which alter its form were described by Valsalva as the tragicus, antitragicus, helicis major and minor, transversus and obliquus auriculae. These muscles are well developed in animals, in which the pinna is capable of a number of expressional movements, but in man they are rudimentary and practically disused, few people (of whom Johannes Müller was one) being able to move their ears at will. So that while, anatomically speaking, the pinna is a typical organ, containing all the parts corresponding to those in other mammals, physiologically it is an organ that is undergoing functional retrogression, and has almost entirely lost the significance it possesses in other animals. Recently (1911) Ch. Fernet has proposed to cure certain forms of semi-deafness by means of *auricular gymnastics*, the aim of which is by appropriate exercises to recover the voluntary functions of the external muscles of the ear.

In order fully to understand the functions of the pinna it is desirable to study it, in the first place, not in man, but in an animal in which it is highly developed, *e.g.* the ass, where its function is that of a trumpet, which collects and condenses the sound-waves. If we apply a long trumpet to our ear, we recognise at once that it is a great help in hearing; the ticking of a watch can be heard at a much greater distance than with the unaided ear. The sound-waves which enter the large aperture of the trumpet with the air are reflected along its walls, so that the waves that reach the meatus are exaggerated. The ears of donkeys and horses, which are mobile, can moreover be turned towards the source of the sound, and thus fulfil the function of hearing-trumpets, whatever the position of the animal. In addition they have dilator and constrictor muscles, so that they can increase or diminish at will the intensity of the sound-waves that reach them.

The human ear, on the contrary, is ill-adapted to this purpose. Its form is very unlike a trumpet, and it has become immobile from disuse. The small importance of the human pinna in audition is shown in the fact that its removal affects the delicacy of hearing very little. If the inequalities of the pinna are filled up with wax or plastidine, this has practically the same effect as amputation of the lobe. Schneider found that audition was slightly diminished; Harless and Esser noticed hardly any difference. Experiments made by Gradenigo on an individual with normal hearing who had lost a lobe showed that the perception of weak, high tones, *e.g.* the ticking of a watch, was facilitated, while loud, deep tones were not perceptibly reinforced. Hence it is clear that a large portion of the sound-waves that reach the

pinna are reflected outwards, and do not sensibly increase the number of those that penetrate the meatus.

If the pinna were placed at an angle of 40° directed forwards it would certainly fulfil its function as an auditory trumpet much better, although psychiatrists regard the protruding ear as a morphological sign of degeneration, and aesthetic considerations would, in any case, depreciate such an advantage. Those who are hard of hearing, however, instinctively use their hand to bend the lobe forward, and thus make it fulfil the office of a sound-collector.

It has been said that the cartilage of the ear may serve as an elastic lamina to receive the sound-waves and transmit them through the bones to the internal ear. But if the meatus is stopped with wax and a watch applied to the pinna we can scarcely hear its ticking, while if it is applied to the mastoid process the sound becomes plainly audible; the cartilages of the lobe are consequently poor conductors of sound.

Is the pinna of any importance in recognising the direction of sounds? The appreciation of the direction of sound will be considered later in discussing binaural audition. The pinna undoubtedly has a certain importance in this connection: when we turn the ear towards the source of a sound, it is under the most favourable conditions for reflecting the wave towards the auditory meatus. When the sound comes from in front, and still more when it comes from behind, the ear is in an unfavourable position. If we use one ear only, while the other is stopped with wax and the eyes blindfolded, we are able to judge correctly of the direction of a sound, by observing how its intensity varies when we move our head in different directions.

Weber maintained that we could judge the direction of a sound by means of the pinna because the sound-waves excite its tactile organs. But every-day experience teaches that the sound-waves in the air excite our sense of touch only when they are of extreme intensity, even in regions in which the body is far more sensitive than is the skin of the auricle.

Buchanan and, at a later time, Kuss and Duval, Beaunis, and Gellé held that the pinna, independent of the movements of the head, reflects towards the meatus the sound-waves that impinge upon its anterior surface, and arrests those which reach its posterior surface. There would thus be an area behind the pinnae in which the vibrations would have difficulty in reaching the ear, and this could be utilised to discover whether the source of sound lay before or behind the head.

To demonstrate this fact Gellé pointed out that if a watch is held horizontally to the ear, first in front, then at the side, then behind the head, and is gradually moved farther away, so as to discover the distance at which the ticking can be appreciated, it is easy to show that this distance is least behind the ear and

greatest when the watch is held laterally to the head in the axis of the meatus. Gellé demonstrated the function of the pinna in appreciating the direction of sounds by a very simple experiment. If the pinnae are eliminated by inserting the two ends of a rubber tube 50 cm. long into the auditory meati, so as to close them completely, and a watch is then placed at the centre of the loop after blindfolding the subject's eyes, the same sensations of sound are received in both ears, and they do not alter if the rubber loop is placed above or behind the head.

Another older experiment of Weber confirms this. If the two lobes are bandaged closely to the skull, with closed eyes we are no longer able to distinguish the forward or backward direction of a sound, because the conditions of the conduction of sound in both directions have become approximately equal.

Weber further noticed that if the hands are placed in front of the ears, like horns directed backward, then with the eyes shut the sound of a tuning-fork placed in front of the head seems to come from behind. This is due to the diminution of the tone by the shield formed of the hands, just as, under normal conditions, the shields are represented by the projecting posterior surface of the lobe.

The canal or external auditory meatus which extends from the concha to the tympanic membrane conveys the vibrations of sound to the middle chamber of the ear. It is 23-32 mm. in length. The calibre of the passage is smallest in the osseous part of the canal, and at a few millimetres from the tympanum it becomes wider again. It has a somewhat tortuous course, so that to look through the meatus at the tympanum in adults the lobe must be pulled a little upward and backwards. The skin that covers it is provided in the outer portion with hairs and sebaceous glands that secrete cerumen. The thick subdermal tissue is rich in convoluted tubular glands similar in structure to the sweat glands, which do not seem concerned in the secretion of cerumen, as is often supposed.

The external meatus may be regarded as an organ for the protection of the middle and inner ear. Its tortuous course, the sensitive hairs at its entrance, and the cerumen with which its surface is smeared, make it difficult for insects to penetrate into the canal. The wax further serves to keep the tympanic membrane from drying up, and makes it supple. The meatus is also a protection against variations of temperature.

Lastly, the external auditory meatus, like all hollow spaces, can function as a resonator, as well as a conductor, of sound-waves. According to Helmholtz and Hensen the proper tone of the auditory passage is too high (between *c* and *a* of the fourth octave) for it to have any perceptible effect on hearing.

III. The membrana tympani is attached obliquely at the end

of the auditory meatus to a special bony ring, at an angle of 55° from above and outwards, down and inwards (Fig. 76). It is slightly stretched, and ellipsoid in form, with a maximal diameter of 9·5-10 mm. and a minimal diameter of 8 mm. Its oblique position provides a more extensive surface, and allows the play upon it of a larger number of vibrations. Moreover, it is not stretched in one plane, but a little below its centre is drawn inwards by the handle of the malleus which is attached to it, thus forming a conical elevation towards the cavity of the tympanum,

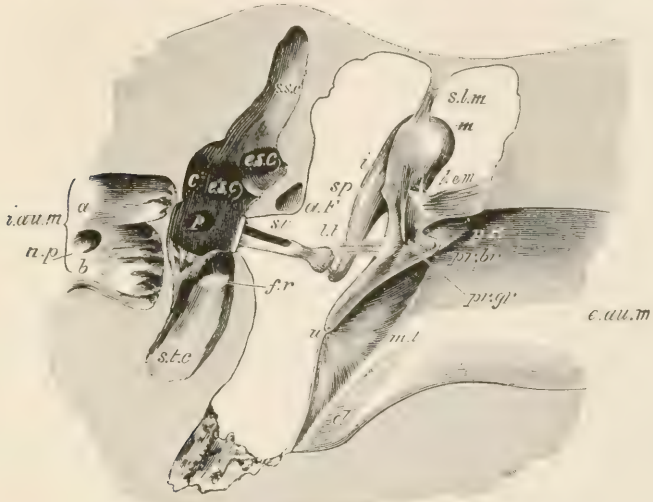


FIG. 76.—Profile view of left membrana tympani and auditory ossicles from before and somewhat above. Magnified 4 times. (E. A. Schäfer.) The anterior half of the membrane has been cut away obliquely. *m.*, head of malleus; *sp.*, spur-like projection of lower border of its articular surface; *pr.br.*, its lateral process; *pr.gr.*, root of processus anterior, cut; *s.l.m.*, suspensory ligament of malleus; *lem.*, its lateral ligament; *t.t.*, tendon of tensor tympani, cut; *i.*, incus, its long process; *st.*, stapes in fenestra vestibuli; *e.au.m.*, external auditory meatus; *pR.*, notch of Rivinus; *m.t.*, membrana tympani; *u.*, its most depressed point or umbo; *d.*, declivity at extremity of external meatus; *i.au.m.*, internal auditory meatus, *a* and *b* its upper and lower divisions for corresponding parts of acoustic nerve; *n.p.*, canal for nerve to ampulla of posterior semicircular canal; *s.s.c.*, ampullary end of superior canal; *p.*, ampullary opening of posterior canal; *c.*, common aperture of superior and posterior canals; *e.s.c.*, ampullary, *e'.s.c.*, non-ampullary end of lateral canal; *s.t.c.*, scala tympani cochleae; *f.r*, fenestra cochleae, closed by its membrani; *a.F.*, canalis facialis (aquaeductus Fallopii).

and presenting a convex surface outward, towards the meatus, especially in the lower segment. At the upper end the conical lateral process of the malleus bulges out towards the auditory meatus.

The membrana tympani is about 0·1 mm. thick, and consists of fibrous tissue with radial fibres at its periphery and annular fibres within, covered externally by a very fine prolongation of the skin, internally by simple pavement epithelium. Notwithstanding its delicacy it is extremely resistant and practically inextensible.

The chain of ossicles consisting of the malleus, incus, and stapes (Fig. 77) makes the anatomical connection between the membrana tympani and the fenestra ovalis, and forms a single apparatus for receiving the aerial vibrations and transmitting them to the fluid of the labyrinth.

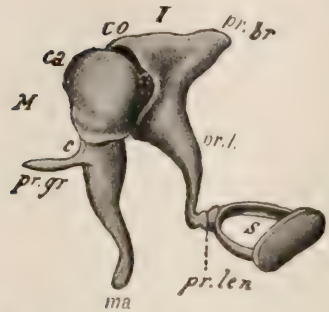


FIG. 77. — The chain of auditory ossicles. *M.*, malleus; *ma.*, manubrium attached to membrana tympani; *ca.*, capitulum articulating with incus; *c.*, cervix; *pr.gr.*, processus gracilis or lateralis, partially converted in adults into ligament; *I.*, incus, forming an amphiarthrosis with head of malleus; *ca.*, body; *pr.br.*, processus brevis; *pr.l.*, processus longus capped by the lenticular process; *pr.len.*, for articulation with head of stapes; *S.*, stapes with cavity for articulation, a short neck, two crura, and a base fitting into the fenestra ovalis.

The handle (manubrium) of the malleus is firmly united by fibrous tissue to the tympanic membrane (Fig. 78). This ossicle is further fixed by two ligaments, one anterior, the other posterior, which confine its movements, and only permit it to make slight excursions from without inwards in an axis through its neck, so that when the handle faces inwards its head moves in the opposite direction.

The incus is attached to the tympanic cavity by a ligament inserted on to its short process. It articulates with the head of the malleus by a saddle-joint, with a very thick fibrous capsule. At the lower edge of its articular head the malleus forms a kind of spur which, when the manubrium moves forward, makes with the incus a single, rigid piece, called by Weber the angular lever, which moves round the common axis formed by the ligaments of the malleus. The rotation of the two ossicles round this axis takes place in a plane vertical to that of the membrana tympani. As the long process of the incus is about $\frac{1}{3}$ shorter than the handle of the malleus the excursions of its end must be correspondingly smaller and more powerful.

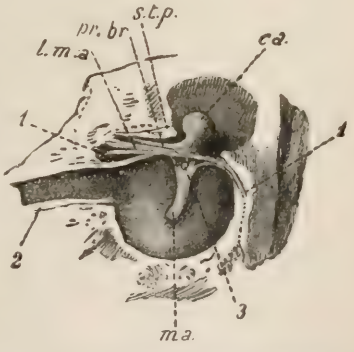


FIG. 78. — Membrana tympani attached to malleus viewed from the inner surface. (Nagel.) 1, Chorda tympani passing through tympanic cavity; 2, Eustachian tube; 3, insertion of tendon of tensor tympani; *s.t.p.*, spina tympanica posterior; *pr.br.*, short process of malleus; *l.m.a.*, anterior ligament of malleus; *ca.*, head; *ma.*, manubrium adherent to membrana tympani.

The stapes is attached by an almost rigid articulation to the tip of the lenticular process of the incus, so that the excursions of the latter are transmitted to the fenestra ovalis, with which the stapes is connected. The excur-

sions of the stapes must, as shown above, be smaller, and at the same time more powerful than those of the tympanic membrane; according to Helmholtz and Politzer they do not exceed 0·07 mm., according to Bezold 0·04 mm.

As the excursions of the chain of ossicles caused by the sound-waves are so small, no change takes place in the position of the articulations. These are only altered by reflex activity of the muscles of the malleus and stapes, when more extensive movements of the membrana tympani occur.

We must now inquire more closely how this apparatus, formed by the tympanic membrane and chain of ossicles, functions as the receiver and transmitter of vibrations. When the sound-waves impinge on it, the tympanic membrane is readily thrown into vibration, on account both of its delicacy and inextensibility and of its low tension, owing to which it offers little resistance. Experiment shows that—like the membranes of the telephone and phonograph—it vibrates in unison with the different tones of the musical scale, *i.e.* it follows the vibrations of the air exactly, without reinforcing tones of any given pitch. Politzer (1864) first demonstrated this directly by experiments on the tympanic apparatus of the human dead subject. After opening up the tympanic cavity, he attached to the chain of ossicles, or directly to the surface of the tympanum, a glass thread or straw, the free end of which recorded on a moving drum the excursions produced by tones of different pitch; these were transmitted to the tympanum from organ pipes, communicating with Helmholtz resonators, which were connected by a rubber tube to the external auditory meatus of the subject. By this method he obtained very definite curves, not only of the simple tones, but also of the compound tones, resulting from the superposition of the different partials.

Lucae (1864) obtained similar results on conducting the tones through the bones instead of through the external auditory meatus of the dead subject. He thus demonstrated that when we perceive the note of a tuning-fork applied to the bones of the cranium, the effect is due not merely to direct transmission of the waves from the bones to the labyrinth, but also to the intervention of the tympanic apparatus. Politzer confirmed this by another ingenious experiment.

As the lever constitutes a load which disturbs the vibrations of the ossicles, Buck (1870), under the direction of Helmholtz, made observations of the excursions produced by blowing into the meatus; he observed the excursions directly under the microscope, and measured their amplitude. On illuminating the interior of the tympanum with a strong light, he found that the membrane of the fenestra rotunda vibrated with the chain of ossicles, and that the excursions of the ossicles persisted after

destruction or perforation of the fenestra rotunda, and after section of the tendons of the malleus and stapes muscles.

Microscopical observations on the oscillations of the tympanic apparatus were subsequently repeated by Burnett (1872), Politzer (1873), and Mach and Kessel (1874). By means of the stroboscopic method, the two latter brought out certain important particulars, as for instance that the fenestra rotunda bulges outwards when the plate of the stapes dips in towards the vestibulum. When very high tones are employed, the excursions of the ossicles become too small to be visible.

Mach and Kessel further observed the movements of the tympanic apparatus in the living animal, after gilding the membrana tympani (1872). Berthold almost simultaneously made similar observations upon living human subjects by the manometric flame method, using the external auditory meatus as a gas-chamber. On applying the tuning-fork to the cranium he obtained good vibrations of the flames in the swinging mirror. Nagel and Samojloff (1898) confirmed these results. They also carried out the same experiment on the head of an animal, using the tympanic cavity as a gas-chamber. Vibrations of the flames were obtained not only on conveying tones or sounds of ordinary intensity to the auditory meatus, but also in speaking or conversing under the breath, which proves the exquisite mechanical sensibility of the tympanic apparatus.

In comparison with these results obtained by admirable experimental methods some more recent experiments carried out by Nuvoli (1907) on the human temporal bone are of less value, but as they present certain new details they deserve a brief description. After opening the roof of the tympanum without injuring the ossicles and their ligaments, he cut the tendon of the tensor tympani, attached to it a thread 30 cm. in length, and fixed the other end of the thread to the centre of the membrane of a filter-shaped stethoscope, connected by two rubber tubes with the observer's ears. On bringing a watch near the external auditory meatus of the anatomical preparation, and lightly stretching the thread so that the tension of the tympanic membrane is somewhat increased, the observer plainly hears the ticking of the watch. The same result is obtained if, instead of tying the thread which connects the tympanic apparatus with the binaural stethoscope to the tendon of the malleus muscle, it is attached to the tip of the long process of the incus, after removing the stapes and resecting the portion of the inner wall of the cavity, above the fenestra ovalis. The ticking is also distinctly (though feebly) perceptible if the thread is attached to the centre of the stapes, after dividing the petrous bone so as to open up the cavity of the vestibule widely. These three experiments give no positive results if the tympanic membrane has been put out

of action by incising or perforating it with a cautery, or when the articulations of the ossicles have lost all their mobility by desiccation, or when the thread is attached to some other point of the temporal bone. But if the tympanic apparatus is thrown into vibration by stronger sound-waves, *e.g.* from a tuning-fork, instead of by the low ticking of a watch, the anatomical preparation will vibrate in all its parts, and the thread carries the sound-waves to the observer's ear even if it be applied to some point of the bone beyond the chain, or to the chain, even when the tympanic membrane is freely perforated, or the chain immobilised or anchylosed by desiccation. In such cases the general vibration of the bones conceals the functional importance of the tympanic apparatus.

The above experiments as a whole give direct proof that the tympanic membrane with the chain of ossicles is capable of vibrating and transmitting sound-waves of different pitch and minimal intensity. It is therefore more delicate than any human invention to facilitate the propagation of sound-waves. Marvellous as are these artificial instruments no telephone, microphone, or gramophone exists that is capable of receiving, transmitting, or reproducing the tick of a watch at several metres' distance, or whispered conversation, or the innumerable sounds and tones of lower intensity by which we are surrounded, all of which are conducted to the labyrinth of the tympanic system.

What is the mechanical explanation of this fact? How is the tympanic membrane capable of vibrating in consonance with the different tones of the musical scale, and of reproducing and transmitting the irregular vibrations of even the lowest sounds? It is obvious that the tympanic membrane behaves quite differently from membranes distended in one place only. When any such membrane, as a drum, is struck it gives out a definite note, the pitch of which falls when the size of the membrane is increased, and rises with increase of its tension. When a tone is produced near it, in which the number of vibrations coincides with, or is a multiple of, those of its proper tone, it vibrates by influence. But if the tone produced is of different pitch from that to which the membrane is tuned, its secondary vibrations cease, and it remains at rest. If the same happened with the tympanic membrane, if it vibrated strongly when the vibrations of the external tone coincided with or were a multiple of those of its proper tone, and little or not at all when the external tone deviated from its proper tone, there would then be an enormous inequality in the auditory perceptions, and the functions of the cochlea would be seriously affected, particularly from the musical point of view. It is evident that conditions exist in the tympanic apparatus which render it capable not only of vibrating to the different notes of the scale, but also of reinforcing every kind of regular or irregular periodic vibration; in other words, the tympanum functions as a

resonator that is tuned to every note of the scale. Observation shows, indeed, that under normal conditions our ear is capable of perceiving, with almost equal accuracy, all the notes of a scale that extends from 30 to 4000 vibrations per second. In accounting for this fact, Helmholtz laid great stress on the funnel-shaped form of the membrana tympani, owing to which there is unequal tension at its central or more or less peripheral parts, as well as on its load, formed by the auditory ossicles which damp its after-vibrations in the same manner as the contrivance used on the piano for damping the vibrations of the strings. According to Helmholtz the ear contains a very perfect apparatus for damping: we are able to distinguish about ten different notes per second. This rapid damping evidently depends not only on the chain of ossicles, but also on the endolymph.

Hensen, in developing Helmholtz' theory, assumed that the tympanic membrane may from its special structure be regarded as a resonator producing an infinite number of proper tones, like the membrane of Hensen's phonautograph, which is curved like the tympanum, and is fixed in one of its radii by a solid body corresponding to the malleus.

Fick, too, attempted to imitate the tympanic apparatus by artificial models, and found them capable of reproducing and reinforcing a multiplicity of sounds and tones. He hoped by these experiments to elucidate the mechanism of the tympanum, starting from the hypothesis that it is capable, when affected by different tones, of vibrating separately in its different sectors, as though composed of a corresponding number of strings of different length and tension. But, as Hensen correctly observes, the tympanum is so firmly woven together that it is impossible to admit the isolated movement of its respective radial fibres.

The ability of the tympanic membrane to vibrate in unison with the different musical notes is consequently still unexplained. We can construct mechanical contrivances which have approximately the same power—the resonance boxes of musical instruments, which reinforce all sounds, being the best example—but no mechanical theory can at present be put forward.

The movement of great amplitude and limited force, writes Helmholtz, which reaches the tympanic membrane from the external air in the form of a sound-wave, is transformed by the tympanic apparatus into a wave of limited amplitude but greater force, and transmitted to the perilymph. The end of the malleus represents the longest arm of the lever, and the pressure of the stapes is one and a half times greater than the force which presses the end of the manubrium inwards. On transmitting the movement of the incus to the stapes, there is a further considerable reduction in the amplitude of the vibration, with a corresponding increment of force. The stapes presses on the fenestra

ovalis; the labyrinthine fluid enclosed within bony walls can move in no other direction than towards the fenestra rotunda with its yielding membrane. The converse process takes place on diminishing the pressure in the auditory passage.

To determine the amplitude of movement of the different parts of the tympanum when impinged on by sound-waves Bezold (1897) carried out a series of accurate researches, by inserting a small manometer into the labyrinth of the dead subject. With the tympanic cavity open, the maximum movement of the stapes in consequence of the oscillations of pressure in the auditory passage averaged 0·04 mm. Of this movement a quarter consists of the incursion, three-quarters of the excursion. The maximal movement of the handle of the malleus is about 0·76, one-third being incursion, two-thirds excursion. The corresponding maximal movement of the tip of the long process of the incus is 0·21 mm., of which one-third is incursion, two-thirds excursion. In the isolated fenestra ovalis the movements of the plate of the stapes, when the tendon of the stapedius muscle has been preserved, are about 0·063 mm., and are fairly equal in both directions. The mobility of the membrane of the fenestra rotunda is about four times greater than that of the plate of the stapes in the fenestra ovalis.

Bezold observed that in dead subjects the excursions of the chain of ossicles are more ample than the incursions, which, as he himself remarks, is difficult to reconcile with the exact transmission of sounds; and it cannot occur during life under normal conditions. It is caused by the fact that in the dead subject, owing to the decreased tension of the internal muscles of the ear, the articular surfaces between the malleus and the incus are able to glide upon one another, because the spurs do not catch. Normally the incus and stapes are closely pressed together in every position by the tone of the muscles which pull the tympanic membrane and the handle of the malleus inwards.

IV. It is obvious from their anatomical relations that the internal muscles of the ear, the tensor tympani and stapedius, regulate the position of the ossicles, and thus affect the tension of the tympanic membrane and the pressure of the labyrinthine fluid.

The musculus malleolaris or tensor tympani (Fig. 79), which was discovered and physiologically interpreted by Eustachius, takes origin in a bony canal above the Eustachian tube, and its tendon curves at a right angle to be inserted on the malleus, a little below its axis of rotation. When the muscle contracts, the manubrium is displaced into the tympanic cavity, and the tympanic membrane and ligaments of the malleus are drawn inwards and tightened, while the perilymph is compressed by the stapes which stretches the membrane of the fenestra ovalis. The

motor nerve of the muscle comes from the motor portion of the trigeminus through the otic ganglion. Ludwig and Politzer were able to observe this movement, when the fifth nerve was stimulated at the base of the cranium.

Helmholtz regarded the tensor tympani as a tightly stretched elastic ligament, the tension of which could be greatly increased by the contraction of the muscle. The effect of this contraction is to make the articulation of the ossicles more rigid and to moderate the vibrations of the tympanic apparatus for loud, deep tones, which obviates undue pressure on the endings of the cochlear nerves. This protective function of the tensor tympani has been compared with that of the sphincter iridis, which as we

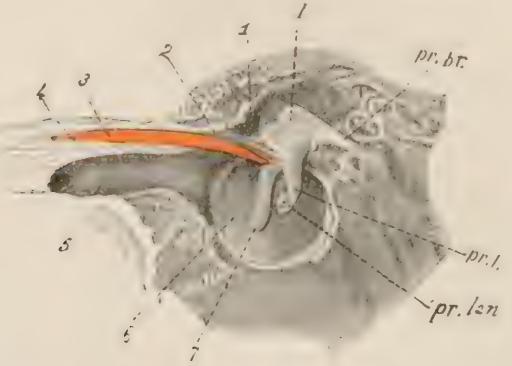


FIG. 79. Course of tensor tympani muscle. 1, Chorda tympani; 2, tendon; 3, tensor tympani; 4, septum, dividing belly of muscle from the Eustachian tube; 5, Eustachian tube; 6, membrana tympani; 7, tip of manubrium, corresponding with umbus of membrana tympani. *I.*, incus; *pr. br.*, short process; *pr. l.*, long process; *pr. len.*, lenticular process for articulation with stapes.

shall see limits the number of rays that penetrate the eye, and adapts it to different intensities of light.

Numerous observations and experiments have been made upon man in health and in disease in support of this theory of the protective functions of the tensor tympani. Destruction of its tendon by disease increases the amplitude of the vibrations of the ossicles, especially in the direction of excursions toward the auditory passage (Bezold). Sometimes after tenotomy the patient complains for many days of hyperaesthesia to high tones of normal strength (Kessel). Helmholtz and Politzer noticed in yawning that hearing was reduced for low tones, which they referred to the associated contraction of the malleus muscle. Some people are able voluntarily to contract this muscle by raising the soft palate. During contraction the low and middle tones are enfeebled, particularly if they are very loud (Nagel and others). Similar results were obtained on anatomical preparations

of man and other animals on pulling the tendon of the tensor by a thread (Politzer, Lucae).

The contraction of the tensor muscle usually takes place reflexly. The sensory paths of the reflex are provided by the acoustic nerve (Hammerschlag): the stimulus is the increase of intra-labyrinthine pressure (Politzer).

The protective function of the tensor muscle has been opposed by the fact that it is not thrown reflexly into tetanic contraction during the whole time that the vibrations of the tympanic apparatus have to be moderated. Hensen and Stricker showed that during audition tetanic contractions of the tensor tympani do not occur, but only simple twitches (as seen on pushing in a fine needle to make a lever arm); these seem to promote the perception of tones, because the tympanic membrane thrown into movement by the muscle vibrates more easily for high tones than the membrane at rest. They further saw in dogs and cats, when the tympanic cavity was opened, that the contraction of the tensor occurs only at the commencement of a tone, and subsequently diminishes and ceases though the tone persists. Bockendahl (1880), a pupil of Hensen, sometimes obtained tetanic contractions, which persisted for the duration of the tone. Without denying the possibility of this fact, Hensen believes that it depends on imperfect fixing of the needle. In fact Pollack (1886) confirmed Hensen's results in a new series of experiments on the functions of the tensor tympani, and invariably obtained only a simple momentary contraction at the commencement of the sound. He further saw that the reflex contractions of the tensor are feebler to low notes, and increase with increasing pitch. When the labyrinth is destroyed the contractions of the muscle become less, but do not cease entirely. After destruction of both cochleae all contractions of the muscle and all movements of the needle stuck into it cease.

Ostmann (1898), by the otoscope, observed in patients with ear-disease the reflex traction of the tympanum which is produced by high notes and loud, unpleasant sounds, owing to the contraction of the tensor. He further observed that in man it is mainly or exclusively high tones that reflexly excite the tensor.

These facts taken collectively make the protective function of the tensor tympani very doubtful.

As early as 1863, Mach, from theoretical considerations, maintained that the tensor tympani produced an *accommodation* of the tympanum, which he based on the supposed power of this muscle to alter the tension of the tympanic membrane so as to adapt its vibrations to different tones. On this theory there must for each tone of given pitch be a corresponding degree of contraction of the tensor. But we have seen that, independently of any active intervention of the tensor muscle, the

tympanic apparatus, owing to its peculiar form, supplies the chief part of what is theoretically requisite, in order that it may vibrate to the different notes of the scale. Mach himself failed after many fruitless attempts to establish any experimental basis for his theory, and gave it up. In this direction the experiments of Schapringer (1870) seem to be conclusive. He was able to contract his tensor muscle at will and found with a suitable manometer introduced into the auditory passage that the tympanic membrane was displaced inwards each time the muscle contracted. But he was unable to detect any evidence of accommodation to different notes of the scale.

On the strength of his observations on curarised dogs, Hensen concluded that the tensor contracts at the beginning of every auditory impression, more vigorously for high than for low tones, and that in audition it damped the consonants, and favoured perception of the accentuated vowels. This implicitly excludes the theory of any *true accommodation*. Many aurists, nevertheless, hold that there is some tympanic accommodation, on the ground that the ticking of a watch is always perceived at a greater distance when it is gradually removed from the ear than when it is approached to it. This liminal difference seems to us to be explicable as a simple phenomenon of attention rather than as an effect of tympanic accommodation.



FIG. 80.—Position of stapedius muscle, made visible by opening the canal which lies within the eminence known as the pyramid. 1, musc. stapedius; 2, its tendon, emerging from the pyramid, to be inserted on the neck of the stapes; 3, tendon of tensor tympani cut short; 4, facial nerve cut across; 5, its canal; 6, promontory in wall of tympanic cavity; 7, head of stapes; 8, Eustachian tube.

The stapedius muscle (Fig. 80) takes origin in a canal of the pyramid. Its tendon issues from the aperture at the apex of that elevation, and is inserted into the neck of the stapes, close to the articulation of that bone with the lenticular process of the incus. Its motor nerve is a small twig of the facial. If the eyelids are closed energetically a sound is heard, which, in all probability, depends on the associated contraction of the stapedius (Lucae).

Gottstein and more recently Ostmann stated that in listening a special sensation of tension is perceived in the ear, which they referred to the stapedius, as this muscle comes into play directly we try to perceive weak tones or noises. In fact, according to Politzer, Eysell, and Mach and Kessel the contraction of the stapedius by pulling on the stapes throws it into an oblique position in relation to the fenestra ovalis, by driving the anterior

part of its plate towards the tympanic cavity, and thus diminishing the pressure in the labyrinth. Simultaneously, owing to the contraction of the stapedius, the obtuse angle between the incus and the stapes becomes somewhat extended—the chain of the auditory ossicles is pushed outwards and the tympanic membrane slightly relaxed, so that the whole of the tympanum becomes capable of more ample vibrations, and the slightest sounds can be perceived. Objections have, however, been raised to Ostmann's theory. The contraction of the stapedius would have to be continuous or tetanic in listening to a prolonged, gentle murmur, which would produce a weakening of hearing owing to limitation

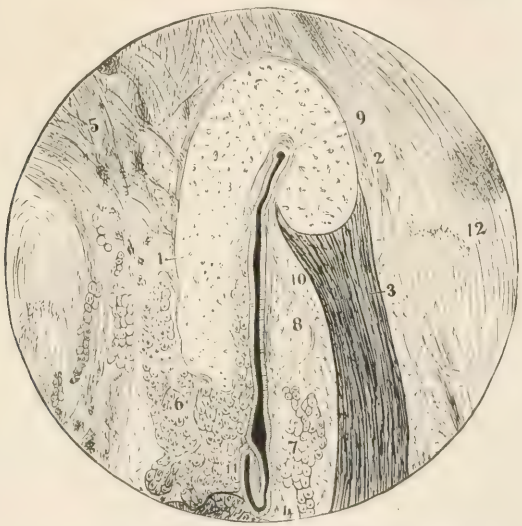


FIG. 81.—Section across cartilaginous part of Eustachian tube. (Rudinger.) 1, 2, curved cartilaginous plate; 3, musc. dilator tubae; to left of 4, part of attachment of levator palati muscle; 5, tissue uniting tube to base of skull; 6, 7, mucous glands; 8, 10, fat; 9, 11, lumen of tube; 12, connective tissue at the side of the tube.

of the movements of the stapes, even apart from the disturbing muscular bruit.

Politzer particularly insisted on the functional antagonism between the tensor and the stapedius, but gave no experimental demonstration of it.

V. The Eustachian tube is a canal about 35 mm. long and 3.5 mm. wide, which connects the tympanic cavity with the upper end of the pharynx. The first portion of the canal is hollowed out of the petrous bone; the second portion consists of a curved plate of cartilage, covered by fibrous tissue and mucous membrane. In sections through the cartilaginous part of the tube (Fig. 81) the cartilage is seen in the form of a hook, the lumen as a slit surrounded by mucous membrane with ciliated epithelium, and

the spheno-salpingo-staphyline muscle or tensor velo-palati is inserted into the hook.

The lumen is generally closed by the apposition of the mucous membrane, aided by secretion, at the narrowest part of the cartilaginous portion. It is only during certain muscular acts, particularly in swallowing and yawning, that the lumen is dilated by the contraction of the tensor palati, which separates the membranous walls of the cartilaginous canal. In some individuals the canal seems to offer very little resistance to opening or to be incompletely closed. In these exceptional cases it is possible on carefully observing the membrana tympani with the otoscope to detect slight movements that coincide with the respiratory rhythm.

According to some aurists this permanent opening of the tube may be artificially induced by scooping it out with a thin flexible sound to a point beyond the isthmus of the canal, that is, the narrowest portion. The effect of this is to diminish the appreciation of deep tones, as also occurs after slight perforations of the tympanic membrane. This shows that the normal closure of the tube, which hinders the air from escaping through it from the tympanic cavity, creates a condition favourable to the transmission to the labyrinth of the vibrations of the tympanic apparatus due to the sound-waves.

That the tube is normally closed is clearly proved by the feeling of painful tension which is experienced in the tympanum on climbing into high regions where the air is rarefied, and which is relieved by occasional swallowing. The same sensation is produced when the tympanic membrane is driven inwards by a high atmospheric pressure, such as may be obtained in a pneumatic chamber. In this case, too, the unpleasant feeling of tension ceases when by swallowing, or by Valsalva's experiment, the lumen of the canal is rendered pervious for a moment, so that the pressure of the air in the tympanum becomes equal to that of the atmosphere.

Valsalva's experiment consists in making a strong expiration after closing the mouth and nostrils, so that air is forced through the tube. Besides this so-called *positive experiment* of Valsalva there is also the *negative experiment* of Toynbee, *i.e.* a deep inspiration with the nostrils and mouth closed, so that air is aspirated out of the cavity. At the moment of aspirating the tympanic air an endotic murmur, due to the stretching of the tympanic membrane towards the interior of the cavity, is produced. When pharyngeal catarrh spreads along the tube, it causes permanent occlusion of the canal with dulness of hearing and an unpleasant sense of tension in the ear, due to the absorption and rarefaction of the air in the cavity, and the consequent *ex vacuo* tension of the tympanic apparatus. Efforts to relieve

this annoyance lead the patient almost instinctively to repeat Valsalva's experiment, that is, to introduce air into the tympanic cavity. This proves that although closure of the tube is very useful in the function of the ear it must not be permanent, but the tube must open now and then in swallowing the saliva that continually accumulates in the mouth, so as to re-establish the normal pressure in the tympanum. Owing to absorption of the air this constantly tends to drop, and thus the vibratory capacity of the tympanic apparatus is gradually lessened.

As the tube is usually closed, the view put forward by many authors that it is designed for the perception of one's own voice is obviously erroneous. This is proved by the observation that the tone of a tuning-fork vibrating inside the mouth is not heard (Schellhammer, Joh. Müller). In cases in which the tube is permanently open, owing to abnormal conditions, or where it is prevented from closing by a catheter (Poorten), autophony may occur, *i.e.* the voice seems to originate and re-echo strongly in the internal ear, instead of in the oral cavity; this causes great discomfort to the patient.

Secchi (Bologna, 1902), in opposition to the generally accepted theory of Helmholtz that sound-waves are conducted by the tympanic apparatus, advocated the view that the fenestra rotunda is the only path by which tones pass from the outer air to the labyrinth. It would exceed our limits to discuss his arguments in detail, but if the main points can be refuted his hypothesis falls to the ground.

He inserted into the tympanic cavity of a living dog a metal cannula, with a two-way stop, connected with a U-shaped manometer 2 mm. in diameter, filled with coloured alcohol. After equalising the pressure of the air contained in the cavity with that of the external air by a half-turn of the screw, he found that at each movement of deglutition made by the animal the fluid in the manometer oscillated slightly owing to the opening of the tube, and the pressure rose suddenly 4 mm. as soon as the act of swallowing was completed and the tube closed again. This positive pressure of the air contained in the cavity (on an average 4 mm. alcohol) is easily explained on the assumption that at the end of the act of deglutition "there is first closure of the orifice of the tube, next of that of the canal, so that the air therein enclosed which cannot escape by the mouth must necessarily enter the cavity and cause a positive pressure." Independently of the mechanism of opening and closing the tube, it happens sometimes when the animal has not swallowed for a long time that the intra-tympanic pressure becomes positive, owing to the action of the internal muscles of the tympanum. At any sudden sound, weak or loud, deep or high, the little manometer then shows a rise of pressure of 4 to 6, 7, 8 mm., in

proportion to the intensity and pitch of the sound, and lasts as long as the stimulus, at the close of which it drops back to 4 mm. This persistent reflex contraction of the endotympanic muscles becomes weaker after administration of chloroform or injection of chloral, and ceases almost entirely after complete curarisation.

The new experimental facts which the Bolognese otologist cites in support of his view are therefore merely that the tympanic membrane with the chain of auditory ossicles and its two muscles represents an apparatus for *reflex accommodation* only; that the transmission of tones to the labyrinth takes place exclusively through the membrane of the fenestra rotunda, which, according to Bezold, is capable of excursions five times as great as the stapes; that, finally, a certain amount of positive pressure in the tympanum, produced by the periodic opening and closing of the Eustachian tube, is indispensable to the normal functioning of the middle ear.

The weak positive pressure in the tympanic cavity of the dog caused by the special manner in which the tube closes at the end of deglutition (even assuming this to be universal in man and all mammals, which is by no means proved) is a fact of little importance. It may be regarded as a slight natural imperfection in the mechanism of the tympanic ventilation, similar to those demonstrated by Helmholtz in the dioptric apparatus of vision. The above discussion on the function of the tensor tympani shows that the most favourable condition for the conduction of tones to the labyrinth is that the endotympanic pressure shall be equal to that of the external air. That acoustic stimuli are capable of evoking persistent (tetanic) reflex contractions of the endotympanic muscles agrees with what Bockendahl assumed, in contradiction to his master, Hensen. But in any case this fact must be taken as the starting-point of new investigations of the doctrine, still *sub judice*, of the inhibitory or protective function of the tensor muscle, and not as evidence for the view that the tympanic apparatus can really become accommodated to different tones and noises.

Lastly, the assertion that conduction of the air-waves to the labyrinth takes place normally by the fenestra rotunda is a flagrant contradiction of the whole of the facts above discussed, and fully confirmed, in support of Helmholtz' theory of the very delicate conducting functions of the tympanic apparatus. It is true that the oscillations of the tympanic membrane may not only be propagated by the chain of ossicles, but may also produce waves of condensation and rarefaction in the air enclosed in the tympanum, so as to impinge on the membrane of the fenestra rotunda, which Bezold showed to be capable of excursions four times as great as those produced in

the fenestra ovalis by the stapes; but the latter have so much the greater force in correspondence with their smaller amplitude that they may render those of the fenestra rotunda ineffective.

It is therefore not proved that under normal conditions the transmission of the acoustic stimulus to the labyrinth occurs by way of the fenestra rotunda, still less that this is the only path that tones take from the external air to the labyrinth. The most that can be assumed (and is held by certain physiologists) is that the vibrations of the air in the cavity may co-operate with those transmitted by the chain of bones. Many otologists (*e.g.* Gradenigo) hold that both the fenestra ovalis and the fenestra rotunda, which are closely connected, may serve in given cases for the transmission of tones; that in very high tones—which are beyond the upper limit of the perceptible scale—transmission through the air of the cavity and the fenestra rotunda may be regarded as predominant, while for low tones, on the contrary, transmission must occur mainly by way of the chain of ossicles. This theory is supported by clinical observations, which show that in pathological processes of various kinds in which there is reason to suspect an accumulation of exudates or a thickening of the membrane of the fenestra rotunda the main functional disturbance is defective auditory perception of the highest notes of the scale, which may amount to an octave or more. On the other hand, according to Helmholtz' theory, it is precisely at the commencement of the first convolution of the cochlea (near the fenestra ovalis) that perception of the highest tones is located.

Under certain *abnormal* conditions the fenestra rotunda is undoubtedly the only path of aerial transmission of the sound-waves to the labyrinth. When the tympanum is perforated there is invariably restriction of the perception of deep tones and a marked diminution of the maximal distance at which accurately measured tones and sounds are appreciable. In fixation or anchylosis of the ossicles, and in immobilisation of the stapes due to any cause without perforation of the tympanum, otologists affirm that hearing is fairly good for high tones, but perception for low tones is reduced. In both cases it is plain that the chain of ossicles cannot function as a special contrivance for the conduction of sound-waves to the labyrinth. Under such abnormal conditions the transmission of air-waves by the fenestra rotunda obviously explains the alterations and limitations of hearing better than Bezold's hypothesis of osteotympanic conduction.

VI. To understand the functions of the Cochlea it is necessary clearly to understand the structure of its most important part, the *cochlear canal* or *scala media*, which contains the very delicate *organ of Corti*, to the cells of which the branches of the cochlear nerve, the true auditory nerve, are distributed.

The cochlear canal is seen in section as a triangular space

(Fig. 82), bounded laterally by the bony walls of the cochlea lined with periosteum, superiorly by Reissner's membrane, inferiorly by a small portion of the lamina spiralis and the basilar membrane. The lamina spiralis terminates in a sickle-shaped edge (*limbus*), which has the form of a C in section, with the under lip projecting and more sharply pointed than the upper. The bay is known as the spiral groove.

The basilar membrane completes the floor of the cochlear canal, being attached on one side to the lower margin of the

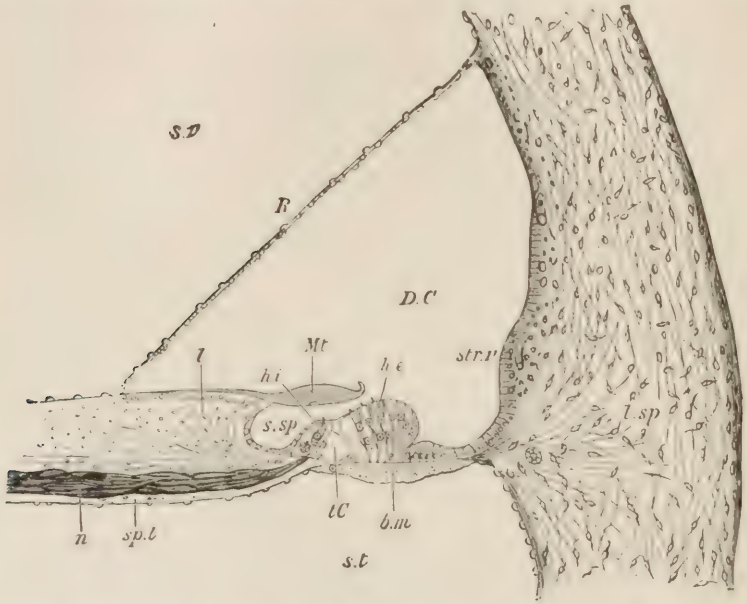


FIG. 82.—Section across the basal turn of the human cochlea. Magnified. (G. Retzius.) *D.C.*, ductus cochleae; *s.v.*, scala vestibuli; *s.t.*, scala tympani; *R.*, membrana Reissneri; *M.t.*, membrana tectoria; *b.m.*, membrana basilaris; *str.v.*, stria vascularis; *l.sp.*, ligamentum spirale; *l.*, limbus; *s.sp.*, sulcus spiralis; *t.C.*, tunnel of Corti; *h.i.*, inner hair-cells; *h.e.*, outer hair-cells; *n.*, nerve-fibres; *sp.l.*, spiral lamina.

limbus, on the other to the spiral ligament, which appears in section to be a triangular projection of fibrous connective tissue attached to the periosteum of the outer wall of the cochlea. It is an important anatomical fact that the basilar membrane increases in width from the base to the apex of the cochlea, while the breadth of the bony spiral lamina diminishes proportionately. According to Hensen, the basilar membrane at the base of the cochlea occupies a narrow cleft about 0·041 mm. across, while at the apex it measures 0·495 mm., that is, about twelve times wider than the base. There are two zones in the basilar membrane: the zona arcuata, to the edges of which the

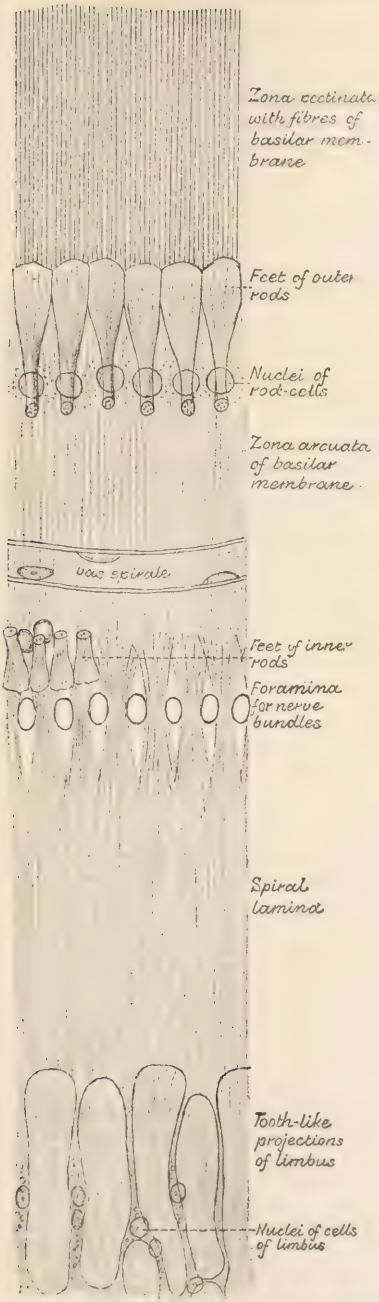


FIG. 83.—Basilar membrane and limbus viewed from above. Magnified. (G. Retzius.)

rods of Corti are attached, and the zona pectinata, extending from the base of the outer rods to the spiral ligament (Fig. 83). The latter zone is somewhat thicker and more fibrous. The basilar membrane, as a whole, is composed of a homogeneous substance, nucleated here and there, with straight elastic fibres running from the spiral lamina to the spiral ligament embedded in it, so that from the surface it appears to be distinctly striated, and in section the fibres are seen as colourless dots in the homogeneous ground-substance (Fig. 84).



FIG. 84.—Tangential section across the zona pectinata of basilar membrane of Guinea-pig. Highly magnified. (Schwalbe.)

On the upper surface of the basilar membrane is the complicated epithelial formation known as the organ of Corti, the true peripheral apparatus which transmits the auditory excitations to the sensorium (Fig. 85). The central part of this apparatus consists of two sets of stiff rod-like bodies standing some little distance apart on the basilar membrane, and inclined towards each other so that they come into contact above. These are the rods of Corti, each pair of which forms an irregular pointed arch, and the double row of inclined columns forms a tunnel along the whole extent of the cochlear canal.

On the inner side of the inner series of rods is a row of epithelial cells surmounted by a

brush of fine, short, stiff hairlets, and external to the outer rods are three or four successive rows of similar but more elongated cells; these are termed respectively the inner and outer hair-cells. The external hair-cells are at some distance from each other. Between each two is a filiform process of the sustentacular cells, or cells of Deiters, which rest upon the basilar membrane. A special cuticular membrane, the lamina reticularis, connects and fixes the upper ends of the hair-cells and the filiform appendices of Deiters' cells. The hairlets project through the openings in this membrane. Externally to the hair-cells and sustentacular cells is a prominent accumulation of large conical epithelial cells which have no hairs, known as the external supporting cells or

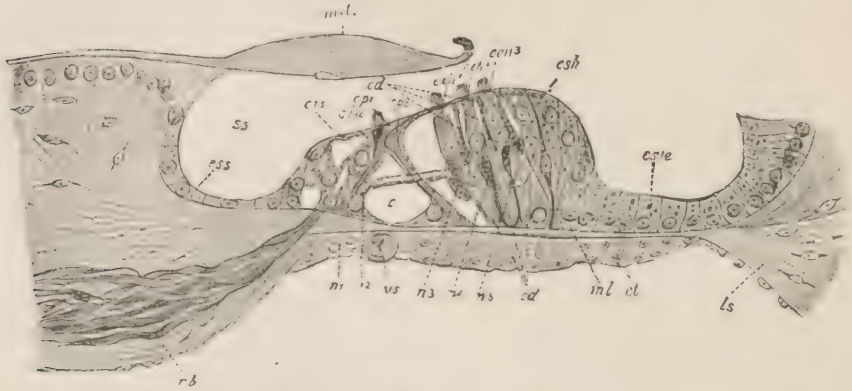


FIG. 85.—Organ of Corti. Human. (G. Retzius.) *m.t.*, membrana tectoria; *s.s.*, sulcus spiralis internus; *r.b.*, nerve-fibres of ramus basilaris; *e.s.s.*, epithelium of sulcus spiralis internus; *c.t.*, connective tissue lining scala tympanica; *v.s.*, vas spirale; *n1*, *n2*, internal branches of nervus spiralis; *n3*, *n4*, external branches of nervus spiralis; *e.p.i.*, cells of internal pillar; *e.p.e.*, cells of external pillar; *t.*, tunnel; *e.i.h.*, inner hair cells; *e.h.*^{1}, *e.h.*^{2}, *e.h.*^{3}, first, second, third row of outer hair cells; *c.d.*, Deiters' cells; *c.s.h.*, Hensen's supporting cells; *e.s.s.e.*, epithelium of sulcus spiralis externus.

cells of Hensen. From these there is a gradual transition to the simple cubical epithelium that lines the most external part of the basilar membrane. The human cochlea, according to Retzius, contains about 12,000 external auditory cells, each provided with some 20 hairlets.

The hair-cells of Corti and the Deiters' cells beneath them are richly innervated from the free endings of the fibres of the cochlear nerve. These fibres pass outwards near the root of the spiral lamina, through a spirally wound ganglionic cord (ganglion spirale), situated in the spiral canal of the modiolus. The cells of this ganglion are bipolar, and each nerve-fibre has one of the cells interpolated in its course (see Fig. 75). From the peripheral side of the ganglion the fibres, which are medullated, penetrate in small bundles into the separate canaliculi of the bony lamina; losing their sheath, they pass through the small apertures near

the point of origin of the inner rods, and wind spirally round the bases of Corti's and Deiters' cells (Fig. 85).

To complete the description of the organ of Corti we must notice in conclusion the tectorial membrane, to which secondary importance has erroneously been ascribed. The membrana tectoria rises on the crest of the limbus in the form of a thin membrane, which subsequently swells in a pad-like projection over the spiral groove, the rods of Corti, and the inner and outer hair-cells (Fig. 86). From the surface it appears distinctly fibrous, with obliquely slanting fibrils and a scalloped edge identical in structure with the subjacent membrana reticularis. Many authors (Gottstein, Hensen, Retzius, Siebenmann) hold that the outer zone of the tectorial membrane terminates in a free edge, which floats in the perilymph a short distance from the ends of the hairlets of the hair-cells. Retzius, however, found in embryos of rabbits and cats that the outer edge of the tectorial membrane is anatomically connected with the most peripheral cells of Deiters, although this union disappears in adult animals. This statement was confirmed by Schwalbe. Others, again, found an indefinite anatomical connection in adults between the membrana tectoria and the underlying organ of Corti (Boettcher, Barth, Czinner, Hammerschlag). More recently (1907) Kishi has shown in some histological preparations that the tectorial membrane is united in adults, too, with the outer surface of the reticular lamina, which often escapes notice because this membrane is normally excessively tense, and retracts, and becomes torn, in the fixing fluid. According to Kishi the normal form of the organ of Corti is that represented in Fig. 87, in which the hairlets of the internal and external hair-cells stand vertically to the membrana tectoria, with which they are in immediate contact. The outer edge of this membrane is connected with the end of the membrana reticularis; when this is stretched, the tectorial membrane is of uniform thickness over its whole extent; finally, the rods of Corti form an almost equilateral triangle with the basilar membrane from which they spring. The increased thickness of the organ of Corti in its outer part in most preparations depends on the elastic retraction it undergoes after rupture of its external border, which also causes deformation of the arches of Corti formed by the rods.



FIG. 86. Surface of small portion of membrana tectoria of human cochlea. (G. Retzius.) *l.z.*, limbus-zone of membrane; traces of cells covering the limbus; *o.z.*, *o.z.*, outer zone showing fibrous structure; *H.*, Hensen's band; *f.*, free reticular edge.

We have already insisted that the transformation of the physical process of sound-vibration into the physiological process of the neural excitation which arouses auditory sensations in consciousness takes place in the cochlea. The impacts transmitted from the tympanic apparatus and the cranial bones act upon the organ of Corti, and excite the endings of the countless branches of the cochlear nerve by means of the hair-cells. The great development of the organ of Corti in man and the higher mammals, as well as clinical and experimental evidence that lesions, such as partial or total destruction of the cochlea, produce incomplete or complete deafness, directly prove this view.

Different theories have been advanced to account for the way in which the vibrations of the plate of the stapes (or vibrations of the bones in general) are capable of affecting the organ of Corti,

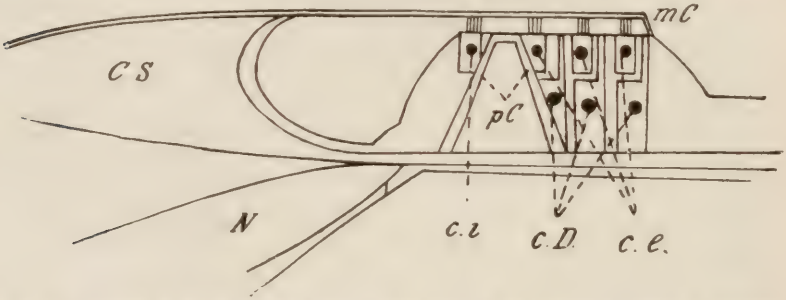


FIG. 87.—Diagram of normal organ of Corti. (After Kishi.) The membrana tectoria is extended in contact with the ends of the hair-cells, and applied to the membrana reticularis.

and exciting the endings of the cochlear nerve by means of the labyrinthine lymph. Helmholtz was inclined in his earlier work to regard the arches of Corti formed by the rods as the cochlear elements designed essentially to vibrate in unison with the tympanic apparatus. Certain structural conditions seem to favour this hypothesis; the arches of Corti, and particularly the outer rods, are able to vibrate freely, because they are surrounded by endolymph, both on the posterior surface facing the tunnel of Corti and the superior surface where a large space separates them from the first series of hair-cells. But as the researches of Hasse show that the organ of Corti in birds and amphibians, while undoubtedly capable of transmitting auditory excitations to the centres, is completely destitute of arches, Helmholtz and Hensen hold it necessary to assume that the basilar membrane, on which the organ of Corti is built up, must necessarily take part in the vibrations that give rise to the auditory excitations. To explain these excitations they assume that the vibrations of the basilar membrane cause the hairlets of the hair-cells to impinge on the

tectorial membrane, and that it is these impacts which cause the active stimulation of the auditory nerve.

E. ter-Kuile (1900) pronounced against this hypothesis. On the strength of anatomical and physical considerations he maintained that the membrana tectoria and the underlying organ of Corti cannot vibrate in opposite directions, but must necessarily vibrate together in the same direction. He assumed that in consequence of the vibrations of the basilar membrane the arches of Corti rotated round the foot of the inner rods, which form the centre of rotation, causing oscillations from above downwards and from below upwards of the entire organ of Corti, including the membrana tectoria (Fig. 88). These oscillations produce a slight flexion of the filaments of the hair-cells, which in their turn act as a stimulus upon the nerve-endings.

To this hypothesis of ter-Kuile the objection can be raised that the basilar membrane is ill-adapted to oscillate from above

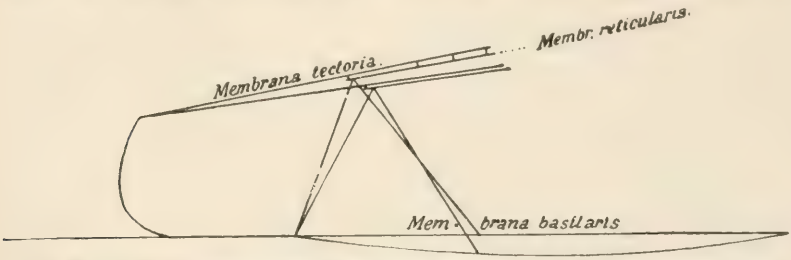


Fig. 88.—Diagram of organ of Corti, and the changes produced in it by the vibrations of the basilar membrane. (After ter-Kuile.)

downwards on gentle impacts of the endolymph. As shown by Retzius (Fig. 85), the basilar membrane is lined on the side of the scala tympani by a dense layer of connective tissue, and on the side towards the scala vestibuli it supports almost the whole organ of Corti, viz. the outer rods, the layer of Deiters' and that of Hensen's cells, and finally the three layers of the external hair-cells or cells of Corti. It cannot therefore be the most mobile part of the auditory apparatus. Siebenmann (1900), and Kishi (1907) concluded from these anatomical considerations that the true vibrating portion is the membrana tectoria, the physical and structural characters of which are such that it can be readily influenced by slight alterations of pressure transmitted by the stapes to the endolymph. It is highly elastic; according to Kishi it is under normal conditions tightly stretched over the organ of Corti; it is surrounded by endolymph, and is in contact solely with the filaments of the hair-cells (Fig. 87). The membrana tectoria is thus eminently suited for transmitting the mechanical stimulus necessary for exciting the hair-cells by means of the slight deformations of the hairlets.

Kishi further points out that if the basilar membrane is to excite the hair-cells by its movements, these should be vertical, not oblique to its plane. Moreover, the inner hair-cells do not lie above the basilar membrane, but are placed above the habenula perforata, so that they cannot be effectively influenced by the movements of the membrane. On the other hand, it is easy to see how movement of the stapes can produce gentle oscillations of the tectorial membrane sufficient to excite the filaments of both inner and outer hair-cells. Like the basilar membrane, the free or outer zone of the tectorial membrane is fibrous in structure, and increases in size from the base to the apex of the cochlea. Lastly, Kishi states that in the first turn of the cochlea the membrana tectoria is not only less wide, but is tightly stretched, while in the apical turn, where it is more than three times as wide, it is loosely stretched. So that from no point of view can it be an advantage to regard the basilar, instead of the tectorial, membrane as the vibrating organ capable of transforming the physical sound-waves into physiological auditory impulses.

On considering the mode of propagation of the sound-waves to the internal ear we find an additional argument in favour of the view that the tectorial rather than the basilar membrane is the vibrating part of the cochlea.

We followed the sound-waves through the tympanic apparatus as far as the membrane of the fenestra ovalis, which moves transversely by means of the plate of the stapes, its range not exceeding 0·04 mm., and throws the perilymph into motion. This, if driven inward, must necessarily exert pressure outwards at some other part of the organ, because fluid is incompressible. Obviously the membrane of the fenestra rotunda may fulfil this object, and many physiologists consider it to be a *counter-aperture*, moving in the opposite direction to the fenestra ovalis (Mach and Kessel). Some have imagined that owing to the impulses from the stapes the fluid of the labyrinth is driven along the scala vestibuli and through the helicotrema to reach the membrane of the fenestra rotunda. But the fallacy of this view is obvious, not only from the fact that owing to the rapidity at which the sonorous vibrations succeed one another there is not time for the wave-movement of the labyrinthine fluid to follow this long course—but also from Pascal's law, according to which pressures exerted in a cavity with rigid walls, closed at one point by a membrane, are transmitted uniformly to all parts of the internal wall. It must be assumed that the sound-waves, on reaching the fluid of the labyrinth, follow no particular course, but are transmitted simultaneously in all directions, through the two scalae of the cochlea. But the waves of impact ascending by the scala tympani can only be transmitted to the endolymph with difficulty, either because they are—at least partially—damped by the yielding of

the membrane of the fenestra rotunda, or by the resistance of the basilar membrane; on the other hand, the waves ascending along the scala vestibuli can easily be transmitted by the thin, loose membrane of Reissner to the endolymph, tectorial membrane, filaments of the hair-cells and terminations of the cochlear nerve. There is accordingly no need to assume any intervention of the supposed vibratory movements of the basilar membrane in order to explain the physiological process of excitation of the auditory nerve by means of the adequate stimulus of the sound-waves. The vibrations of the membrana tectoria suffice.

We still have to solve the far more difficult problem of how the peripheral organ of hearing is capable of arousing auditory impressions with all their distinctive qualitative characters in consciousness. Before attacking this problem, to the solution of which all theories of audition are directed, the physical qualities of sound-waves, and our faculty of perceiving them as such, must be briefly discussed.

VII. A primary distinction in auditory sensations, which has been generally admitted since Helmholtz, is that of *sounds* and *noises*. Although this distinction is sanctioned by common parlance, it is not easy to give an exact psycho-physiological definition of these two terms.

Speaking generally, *sounds* (or *tones* in a wider sense) are the auditory sensations which run an equal, balanced, regular course; *noises* are auditory sensations which, when they have a certain duration and are not merely a single impact or sudden shock, are distinguished by harshness and instability, and are not uniform. The acoustic impressions produced by musical instruments are the best examples of sensations of tone; whispering, whistling, the howling of wind, the splashing of rain, the cracking of thunder, the rattling of a cart, the rasping of a saw, are examples of different kinds of noises. Yet though tones are quite distinct from noises in their extreme forms, these distinctive characteristics are modified in the intermediate forms, and may gradually merge into one another, or the former may mix with the latter in varying relations. Musical tones, also, may create a noise, as when all the keys of a piano are struck together for the range of one or two octaves.

Differences of duration, intensity, uniformity, and above all pitch can be detected, not only in tones, but also in noises. The tones associated with noises are termed harsh, raucous, strident, etc. It may safely be affirmed that both tones and noises are compound auditory sensations, resulting from the mixture of a certain number of elements, known as simple tones.

On investigating the nature of the stimuli that arouse auditory sensations in the ear they appear to the tactile sense to be quivering, to the eye to be vibrating bodies with blurred outlines.

If these vibrations are recorded on a regularly moving surface, tracings are obtained which vary greatly in form according to the nature of the sounding bodies. The tracings of tones have, whatever their forms, one common characteristic, that they are built up of equal and regularly repeated periods. The tracings of noises, on the contrary, lack periodicity and regularity. We know from the results of physical investigation that *simple tones*, *i.e.* the components of compound tones and noises, are pendular or sinusoidal vibrations of elastic bodies, differing only in duration and amplitude. The sensation of *pitch* depends on the duration of the tone or the number of vibrations per second; that of *intensity* on the amplitude of vibration.

It is easily demonstrated by the graphic method, or by the syren, that tones are higher or lower according as the number of vibrations of the sounding body in the time-unit is greater or less. If a writing-point is fitted to the sounding body and brought in contact with the surface of a drum rotating at constant speed, it is easy to count the vibrations in a second, and thus to prove that the pitch of the note is a result of the number of vibrations. It is still easier with the syren to determine the number of vibrations that correspond to a given tone. Seebeck's syren, which is the simplest, consists of a metal disc which has at an equal distance from the centre a given number of equidistant holes, and is fixed to a central axis, on which it can be rotated at uniform speed. By means of a tube communicating with a reservoir of compressed air or a bellows, a blast of air can be driven on to the disc, and rhythmically set free or interrupted, according as the opening of the tube is opposite to a hole or to a section of the disc. These rhythmical interruptions generate vibrations in the air, and thus produce higher or lower tones according to the greater or lesser speed at which the disc rotates. Experience, moreover, shows that the pitch does not change with the alterations in size of the holes in the disc or the pressure at which the air passes through them. It is thus clear that the height of tone depends solely on the number of vibrations per second.

It is still easier to show that the intensity of auditory sensations depends on the amplitude of the vibrations of the sounding body. If a monochord or tuning-fork is made to vibrate, the acoustic sensation, which is very strong at first, becomes gradually weaker, as the amplitude of the vibrations, which is visible at the outset, becomes more and more invisible. At each moment of vibration the intensity of the sensation is equal to the kinetic energy with which the vibrating body passes the position of equilibrium, and this is proportional to the square of the velocity or the amplitude of the vibration.

VIII. The specific capacity of our ear for perceiving in the form of simple and compound tones and noises the regular or

irregular periodic movements of elastic bodies, is confined within certain limits of intensity and pitch.

Many physicists and physiologists have attempted to fix the *lower limit* of auditory capacity—that is, the minimum of pendular oscillations per second necessary to produce an acoustic sensation. Sauveur (1700) was the first who determined the lowest audible sound with organ pipes, and estimated it at 12½ vibrations per second. Cladni (1802) and Biot (1829), who used strings, gave the limit as 16 vibrations. Helmholtz found the note of a tuning-fork audible that gave 26 vibrations per second. Wolf (1871) made the same observation. Preyer (1876) used metal tongues that gave 8 to 40 vibrations, and found that in some particularly sensitive persons the minimal limit was 16 vibrations, in other normal individuals 33. Appunn (1887–88) with his lamella estimated the limit at 9-12 vibrations; Cuperus (1893) with the same method at 10-13; van Schaik (1893) and Battelli (1897) at 24; Gradenigo at 8-12.

In all these researches there is an error of method, since the possibility that the ear perceives harmonic partial tones is overlooked. Recent experiments in fact show that none of the different sources of sound employed are capable of producing single tones entirely free from partials. Not only strings, but also metal tongues, organ-pipes, and even tuning-forks produce tones mingled with harmonic overtones, as may be shown by suitable resonators. Helmholtz recognised that a tuning-fork vibrating strongly at 64 vibrations per sec. gave as many as five partials. To exclude these, Preyer attempted to reinforce the fundamental tone with resonators; but even by this means he failed to separate it from the overtones. In fact resonators to some extent strengthen the partial as well as the fundamental tones. In order to produce a very low tone, free from harmonic partials, Helmholtz loaded the strings with metal weights, so that on sounding they gave only dissonant partial tones which could not blend with the fundamental tone; but with this method the fundamental tone became too weak for the purposes of the experiment.

Accordingly it is not possible to assign any tone of given pitch as the lower limit of audition. Individual differences in the capacity for perceiving tones can be detected even within normal limits of hearing, and the lower threshold of auditory capacity alters considerably with practice and with the degree of attention given by the subject.

Below 40 vibrations per sec. tones lose their musical character and become gradually weaker, indistinct and discontinuous.

Experimental data to determine the *upper limit* of auditory capacity were given by the same authors who endeavoured to establish the lower limit. The earliest (Sauveur, Cladni, Biot, and Wollaston) range from 6400 to 200,000 per sec., but are entirely

unreliable owing to the methods employed. Savart (1830) was the first who obtained more exact results by his dented wheel, which threw a sheet of cardboard into vibration. He found that tones of 24,000 vibrations were still distinctly perceptible. Preyer used Seebeck's syren for the same purpose, and found that 16,000 vibrations per sec. are audible as a very clear note, and that 24,000 vibrations are still perceptible, though feebly so. Pauchon used a Cagnard de la Tour's steam syren for the same purpose. With a steam pressure of 0·5 to 1·5 atmospheres he obtained a limit of perception at 24,000 to 30,000 vibrations; with a pressure of 2·5 atmospheres the limit rose to 36,000, without even then reaching the highest perceptible note.

Preyer repeated these researches with König's sounding cylinders. He found that e and g of the 8th and c of the 9th octave are perceptible, but produce disagreeable sensations, and concluded that the extreme limit of hearing is the e of the 9th octave, which produces a brief and very weak sensation.

The upper limit of audition, also, varies considerably for different normal individuals. Zwaardemaker further noted that it sinks with increasing age, although the figures he has given are too low owing to the imperfections of his method.

Edelmann held that in persons with optimum auditory capacity the entire range of perceptible tones extends over 12 octaves (from 11 to 50,000 vibrations).

But in music excessively high and low tones are both excluded. The deepest note of a large organ consists of 16·5 vibrations (C of sub-contra octave). The highest note of the piano consists of 3520-4244 vibrations (a^4-c^5). The piccolo flute also comprises d^5 (4752 vibrations). But the notes usually employed in music lie within the compass of about 8 octaves (from 40 to 4700 vibrations).

To determine the capacity for perception of the highest notes, which may vary greatly in ear-disease, otologists generally make use of Galton's whistle, which can give a whole series of high notes, from C^4 to the highest tones that lie at the extreme limit of the auditory sensibility of the human ear. The pitch of the tones produced by the instrument can be altered by simply moving the two micrometer screws.

In the most perfect form given by Edelmann to Galton's whistle it consists of two metallic parts. One of these (A,B,D of Fig. 89) is joined to the mouth A by a rubber tube, with an elastic ball or bellows, which provides the air necessary for sounding the whistle. The second part (E,F,G) is the whistle proper; this consists of the tube E, by which the air enters, blown through tube D placed opposite, at a distance that can be varied by the micrometer screw B. The tube E communicates with the body of the whistle F, which consists of a hollow cylinder, the floor of which can be displaced by means of a second micrometer screw G.

The pitch of the tone is in inverse ratio with the length of the hollow cylinder, so that when the screw G is turned in one or other direction a higher or lower tone results. An empirical graduation of the worm of the screw makes it possible to count the number of vibrations in the tones obtained by different positions of the screw.

To produce the highest tones, the opening of the cylinder *D* must be brought near the mouth of the pipe *E* by means of the micrometer screw *B*, which is empirically graduated.

To obtain uniform sounds, it is necessary to employ an air-current of constant intensity. For this purpose a bellows, or better still a blast of constant pressure, must be used.

Just as the scale of perceptible tones is circumscribed within a minimum and maximum number of vibrations in the time-unit, so the capacity of the ear for distinguishing the *difference* between two notes of different pitch is also limited. It is only when the difference between two tones exceeds a certain minimum that we are capable of distinguishing them as different in pitch.

After a few experiments by Delezenne (1825) and Seebeck (1846), Preyer (1876) was the first to solve the problem of the liminal threshold of tone-discrimination by a number of systematic researches with a set of metal tongues. He was able to prove that a trained musical ear is capable of distinguishing between two tones of 500 and 500·3 vibrations, or of 1000 and 1000·5 vibrations; while two tones that differ by 0·2 vibrations only cannot be distinguished with any certainty. Luft (1888) confirmed Preyer's results by a series of tuning-forks with resonators. In the lowest tones the discriminative capacity is less, even for the trained ear. Preyer observed that below 40 vibrations it is not easy to distinguish two tones that vary by one whole vibration; Luft found the threshold of difference for very low tones to be 0·44 vibrations. Persons who are untrained make errors of several vibrations in estimating the difference between very low notes.

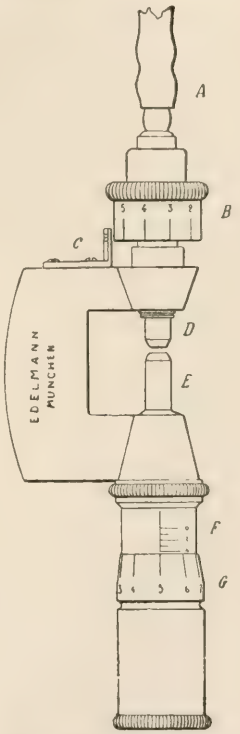


FIG. 89.—Galton's Whistle; Edelmann's new model.

Generally speaking, it may be said that the mean power of discrimination of pitch is much lower than the recognised optimum. Stumpf (1889) found that many people are unable to say which of two tones is the higher, even when they differ by an interval of a third, a fourth, or even a fifth.

It is very doubtful whether the limit of capacity for perceiving the difference between two tones follows Weber's law, *i.e.* is proportional to the number of the vibrations. According to Scripture, very gradual alterations in pitch may amount to a whole tone, without detection even by a musical ear.

IX. Musical tones differ not only in the frequency and intensity of the vibrations but also in other characteristics, which change gradually with the alteration in pitch. Low tones are generally termed "dull," high tones "bright." These distinguishing characters are most marked when the extreme ends of the scale are compared, and gradually become less distinct in the middle tones.

Besides the characteristics of dulness and brightness derived from visual sensation, various spatial ideas are connected with the different tones: bass notes are termed deep, heavy, blunt; treble notes high, thin, and sharp. This spatial character which we connect with auditory sensations agrees with the fact that low tones are given out by large instruments, or by the throat of big animals or of full-grown men; high tones, on the contrary, by small instruments, or little animals, or by women and children. According to Stumpf, however, the spatial character of tones is an inherent property, independent of purely psychological processes of association.

Many physicists and physiologists have observed that the ear is relatively more sensitive to high than to low notes. Helmholtz observed that of two different tones with the same amplitude of vibration the higher tone sounds louder. Charpentier (1890) found that notes lying between f and f^3 with the same amplitude of vibration are audible at a much greater distance in proportion as they are higher in pitch. Max Wien (1903) confirmed this with the telephone. He found that comparatively strong currents were required on the telephone to make the lower tones perceptible. As the tones rise sensibility increases rapidly, and reaches its maximum in the tones of between 1000 and 5000 vibrations, above which it declines again. The lowest notes of large tuning-forks can only be heard at a small distance from the ear, while the high notes of small forks are audible at a distance of several yards. The highest tones give a disagreeable, almost painful sensation, as if the drum were pierced with a needle, and for that reason are not used in music. In conclusion, it may be said that high notes are louder and more penetrating than low notes.

Stumpf described the three characteristics of tones, viz. brightness, fulness, and resonance, which alter gradually with increasing pitch, by the term *tonfarbe* or *timbre* (quality). He thus assumed that not only the compound tones of musical instruments but also the simple tones of which they are built up are distinguished by *timbre* or quality, as well as by intensity and pitch.

It is true that according to the latest researches no instrument exists that is capable of giving out pure tones unmingled with partial notes; but the ear is always capable of distinguishing the quality of the fundamental tone, especially in those instru-

ments in which the partial notes are so weak that they have no musical value. Such are tuning-forks, organ-pipes of the highest tones, and flutes. These instruments may be used to distinguish the quality of the respective fundamental tones.

The *timbre* or quality of musical tones—*i.e.* of compound masses of sound—expresses the particular character by which the different orchestral instruments, including the human voice, are easily distinguished from one another, even when they give out the same note with uniform intensity (see Vol. III. Chap. III.). When a certain musical note is sung and the same note is sounded on the violin, clarinet, flute, piano, and organ, every tone is composed of the same number of vibrations. Yet they can be distinguished by an ear that is but slightly musical, and referred to the instruments which produce them, because the larynx and the various musical instruments give the note a peculiar quality or colour, independently of the number and amplitude of the vibrations.

The attempt to explain the different qualities of tone leads to the idea that these depend on the different *form* of the vibrations produced by the different instruments, which in its turn depends on the number, position, and intensity of the over-tones which summate algebraically with the fundamental tone.

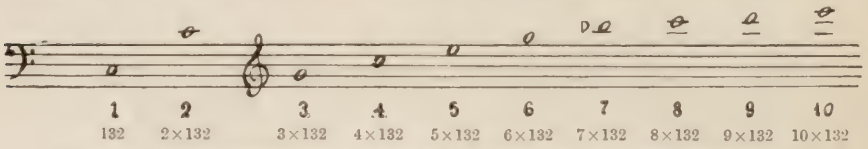
It has long been known to musicians that the separate tones of musical instruments are accompanied by a series of higher tones, known as the harmonics or partial tones of the fundamental tone, which is the lowest of them. When the string of a double bass is made to vibrate over its entire length, a note is obtained in which the trained ear at once recognises complexity, and is able to distinguish a fundamental tone, and that of the octave next above it, which contains double the number of vibrations. This means that while the whole string makes a single vibration, each of its two halves makes two. The proof is given by the fact that if, while the string is vibrating over its entire length, the fundamental note is suppressed by placing the finger in the middle of the string, the octave composed of the vibrations of its two halves, which were not suppressed and which necessarily pre-existed, is distinctly heard.

But when the string vibrates over its whole length, not only the two halves, but also the three thirds, four fourths, five fifths, etc., of the string vibrate synchronously, producing partial tones that are increasingly higher and weaker, and thus less easy to distinguish. The pitch of the partials is determined by the fundamental tone. In proportion as this has one vibration, the first harmonic has two, the second three, the third four, the fourth five, etc. If, *e.g.*, the fundamental tone is a *c*, the series of harmonics will be c^1, g^1, c^2, e^2, g^2, etc. Fig. 90 shows in musical notes the series of harmonic overtones or partials of *c*.

It is seen from this that the intervals between the successive

partial tones are the octave, the fifth, fourth, major third, minor third, major second, etc. They become smaller as the overtones are higher—and as the successive partial tones become weaker and weaker it is obvious that even a trained musical ear will fail to distinguish all the partials contained in a tone. The ear perceives the compound tone as a uniform whole, although it is easy to distinguish the *timbre* of the different instruments, because in each the number and relative intensity of its partial tones vary, and thus result in a qualitative difference in the sounding mass as a whole.

In order clearly to distinguish and determine all the partial tones contained in a compound tone, in other words to analyse its different elementary components, it is advisable to employ Helmholtz' resonators. Each resonator is tuned to a definite note of the scale, and is able to reinforce it. Even though it contains a number of tones proper to itself it resounds with special intensity to the lowest of them when a sound containing this note is struck near it. By applying each resonator to the ear in



[FIG. 90.—Musical representation of the series of harmonic overtones of the note $C = 132$ d.v.

turn, the partials of which a compound tone consists can be strengthened, and become easy to recognise.

Helmholtz' resonators are hollow metal spheres of different diameter with two openings: from one, the larger, a cylindrical prolongation from the walls of the sphere projects a certain distance, and serves to collect the air-waves coming from the sounding instrument and transmit them to the mass of air confined within the walls of the resonator. The second, smaller, opening is diametrically opposite, and a conical lengthening of the walls of the sphere projects a certain distance from it to make connection with the ear of the observer.

The several resonators strengthen and make clearer the partial tones from which the compound tone results, in proportion with the mass of air contained in each resonator. The tones heard from each resonator must therefore vary with its size, and in order to analyse the different tones a complete series of resonators, corresponding to the semitones of the scale, must be provided.

Edelmann reduced the number of resonators to five, with diameters of 350, 150, 80, 45, and 30 mm.; he used the same resonator for analysis of several semitones by placing a series of diaphragms of different diameter upon the receiver. He also improved Helmholtz' resonators by other modifications.

Fig. 91 shows the series of Edelmann's resonators with various diaphragms (*a*, *b*, *c*, *d*, *e*) and the rubber tube *r*, one end of which is to be attached to the resonator, and the other to the observer's ear.

Fig. 92 shows one of these resonators in section. In this *a*, *b*, *c* indicates the section of the walls of the hollow sphere, 1 mm. thick. It is interrupted

at three points of its periphery *A*, *B*, *C*. The opening *A* serves, as in Helmholtz' resonators, to receive the sound-waves; the lumen of this aperture, unlike Helmholtz' resonators, can be altered at will by means of diaphragms (*d*, *e*) which can be screwed to the end of the tube *A*, *F*. On varying the lumen of this diaphragm, the proper tone of the resonator alters, and Edelmann provides diaphragms of different apertures, by which the proper tone of the resonator can be varied exactly from semitone to semitone.

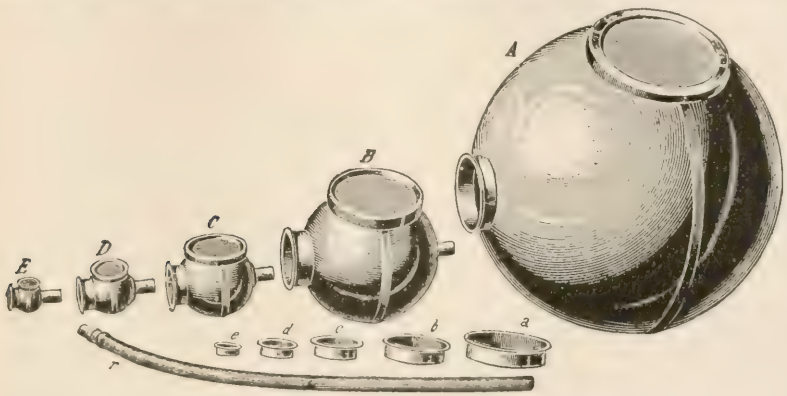


FIG. 91.—Series of resonators; Edelmann's new model.

The semitones which can be analysed by these resonators are 72, and form the 6 octaves from *C* of the contra-octave to *c* of the 4 times accented octave (from 32·33 to 2068·6 d.v.).

The opening *C* serves for hearing, while the opening *B*, which is absent in

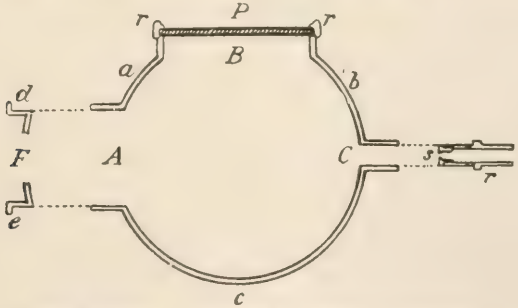


FIG. 92.—Section through one of Edelmann's resonators.

Helmholtz' resonators, is made air-tight by a thin, circular plate of resonating wood, and conducts the sound-waves from an instrument placed directly against it to the air contained inside the resonator. This is particularly advantageous in the analysis of feeble tones, which cannot be analysed with Helmholtz' resonators because their waves are weakened by transmission through the air.

Even without the aid of hearing, the compound nature of tones can be demonstrated physically by the König's flame manometer (Vol. III. p. 131).

For this purpose König constructed an apparatus which consisted of a certain number of resonators, provided with manometric flames, and tuned to the tones of which the number of vibrations stand in the same proportion as the natural series of numbers 1, 2, 3, 4. Each resonator communicates by a rubber tube with a manometer capsule; the burners of these capsules are arranged under one another beside a four-sided mirror, which can be turned with great rapidity round an axis parallel with the direction of the flames.

When a sound is made near this apparatus all the resonators capable of vibrating in unison with the elementary tones contained in the compound tone cause the respective flames to vibrate, and the images reflected in the revolving mirror present characteristic indentations. On the other hand, the resonators of which the notes are not contained in the tone struck remain silent, and the respective flames are unaffected, as shown on the revolving mirror by the appearance of a continuous streak of light. The analysis of compound tones by these manometric flames is a less sensitive method than the direct application of resonators to the tympanum. It only serves in recognising the lower partial tones, because the flames are incapable of vibrating with sufficient rapidity to indicate the rapid oscillations of the higher partials.

The analysis of compound tones into their respective simple component tones is merely the experimental confirmation of a mathematical theorem formulated by Fourier (1822), long before anything was known of the harmonics of the compound tones. He proved that every periodic movement of any form can be resolved into a certain number of simple pendular movements, the periods of which are all multiples of that of the whole movement. The analysis of compound into simple elementary tones by means of resonators shows that Fourier's theorem is not a mathematical fiction, but an expression of actual fact.

As almost all the tones of the various musical instruments, including the human larynx, are compound, and comprise a quantity of partial tones which differ in number and intensity, the differences in *timbre* or quality in all probability depend upon this fact.

Compound tones of different *timbre* may, even when they express the same fundamental tone, be graphically represented by a different complex form of vibration. But it would be inaccurate to say that the perception of the quality of musical instruments depends on the ability of our ear to recognise the different forms of sound-vibration as such. In effect, the complex curve of any given tone undergoes considerable changes in form, owing to simple displacements of the phases of its partial tones (Fig. 93). Repeated experiments show, however, contrary to the opinion of R. König, that such displacements of phase do not sensibly affect

the character of the tone, *i.e.* its quality (Hermann, 1894; Lindig, 1902). Hence it may be concluded that our ear does not perceive the form of the vibration as such, but that it is capable of perceiving the partial tones that result from the analysis of the compound tones. In other words, in so far as the ear is able to distinguish the *timbre* of the different musical instruments, it is capable of analysing tones and of detecting the partials of which they are built up.

X. The fact that the ear is capable of perceiving not only the entire mass of sound, but also the separate elements of many different tones and noises produced simultaneously, is yet more astounding. A musical ear is able to follow the tones of the several instruments of an orchestra. Each note of each instrument forms its waves, which spread in all directions, cross, and are reflected from the surrounding walls, partially extinguished by interference, partially summated and reinforced by coincidence. This whirlpool of waves intermingling in every direction cannot be discerned by the eye, but the ear is quite capable of perceiving it, both as a whole and in its separate elements. All these sound-elements are already mingled when they reach and act upon the drum of the ear, *i.e.* all the component elements are combined in their algebraic ordinates into a very complex vibration. In the same way they reach and act upon the membrane of a phonograph, which inscribes with its needle on the rotating disc the compound curves of vibrations in which are collected all the tonal elements that have contributed to their formation.

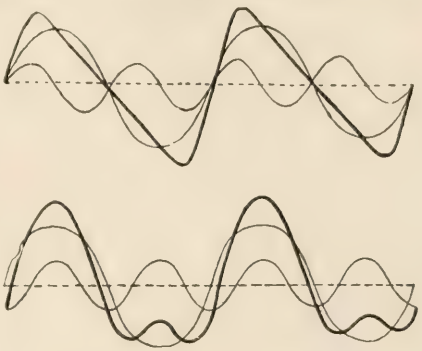


FIG. 93.—Combination of two sinusoidal waves, in which the ratio of amplitude is 2 : 1 (fundamental and octave); in the upper figure there is no dislocation of phase, in the lower there is a dislocation of one-fourth the octave-wave. The two resulting curves, drawn with a heavier line, are very different in form. (After K. L. Schafer.)

These complex resultant vibrations are transmitted as such from the tympanic apparatus to the organ of Corti, where a marvellous analysis takes place which renders us capable of feeling and distinguishing the tones of different instruments, individual human voices, the mixture of tones and noises which constitutes language, the rustling of clothes, the sound of steps in a dance, and the voices of passers-by during the procession of life in a great city.

The best proof of the fact that the elements of a polyphonic mass are not transmitted separately to the internal ear, but are

summated algebraically in the form of a single complex vibration, viz. that our capacity for distinguishing and perceiving them depends on the analytical capacity of the organ of Corti, is given by the phonograph. By letting the needle glide over the indentations of the phonograph disc the same vibrations are reproduced on the membrane as were recorded on the disc; and these suffice to reproduce distinctly the whole of the tones, noises, and voices which had previously aroused them.

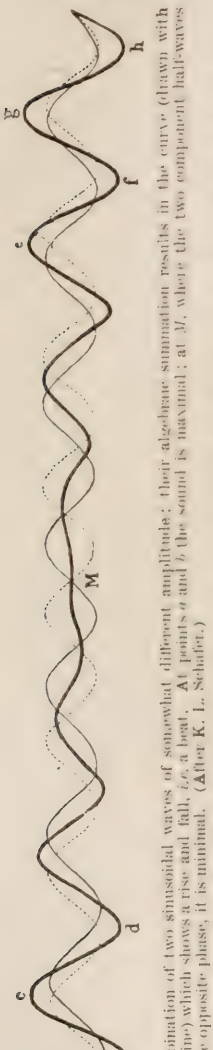


FIG. 94.—Combination of two sinusoidal waves of somewhat different amplitude; their algebraic summation results in the curve (drawn with heavier line) which shows a rise and fall, *i.e.* a beat; At points *a* and *b* the sound is maximal; at *M*, where the two component half-waves are in the opposite phase, it is minimal. (After K. L. Schäfer.)

Physicists and physiologists have made extensive studies of certain fundamental phenomena that may be observed during the synchronous production of a number of tones.

The simplest of these phenomena is the *interference* of sound-waves. When the waves of two tones are superposed, and summate algebraically, there may be increase, diminution, or even extinction of the wave-movement and thus of auditory sensation, according to whether the two waves at their meeting-point are in the same, or in a more or less different, or in an opposing phase. When the two interfering waves have the same pitch, the increase or diminution of intensity, or the extinction of the sound, remains constant, as is easily verified with Helmholtz' double syren.

When, on the contrary, two tones of not quite equal pitch meet simultaneously, that is, when they contain a slightly different number of vibrations, then the two waves do not always meet in the same phase, but there is alternate coincidence and interference of the waves, with a periodic rise and fall in sensation (Fig. 94).

These periodic increments and decrements of auditory sensation are known as *beats*. If there is a difference of one vibration per second between the two simultaneous tones, then during that time they will be once in the equal and once in the opposite phase; in every second there will be a reinforcement and a diminution of intensity, *i.e.* a beat. If the difference between the two tones is two vibrations per second, two beats will be perceptible in each second. Generally speaking, it may be held that two coincident, non-identical tones give rise at each second to a

number of beats equal to m-n, if m and n represent the number of the vibrations of the two tones.

The diagram (Fig. 94) shows the simplest case of two simple simultaneous tones (represented by two pendular or sinusoidal vibrations of different length) which, through their summation, produce a beat. In the central part of the figure, where the positive half-wave of one of the tones coincides with the negative half-wave of the other, there should be almost complete extinction of the resulting tone. In practice, however, this is almost unrealisable, because the tones emitted by the different instruments are always compound, *i.e.* can be resolved into several partial tones: so that during the beat there is never total extinction of the tone, because when the two fundamentals are extinguished, the first harmonics, *i.e.* the octaves, are reinforced. On the other hand, the octaves and successive partial tones of the two different fundamental tones must theoretically produce their respective beats, which will be less perceptible to the ear in proportion as they are less intense.

Beats are also produced when the two simultaneous tones act separately on the two ears (Dove and others). Does this depend on cerebral interference between the two excitations of the auditory nerve, as assumed by Scripture, Wundt, and Ewald, or on the fact that the tone that impinges on one ear is transmitted to the other through the bones, as held by Schäfer, Bernstein, and others? This last interpretation alone seems probable.

When two tones are simultaneously produced which differ more widely from each other, and must therefore theoretically give rise to so large a number of beats that they can no longer be perceived distinctly as such, then in addition to the two primary tones a trained ear can distinguish a third, deeper, note, known as Tartini's tone, because it was discovered by the eminent violinist of that name (1714). This third tone was at first supposed to be a subjective phenomenon, due to the beats, when these attain a frequency so great that they can no longer be recognised distinctly as such. But Helmholtz by calculation showed the objective character of Tartini's tone, which he termed the *differential tone*, because its vibration number is equal to the difference between those of the two primary tones. If, for instance, these are at an interval of a fifth, that is, are in the ratio of 2 : 3, the differential tone is the octave below, since the difference is equal to 1.

Helmholtz referred the formation of the differential tone to the fact that the transmitting medium does not react in the elastic deformations with a force proportional to the displacements, so that the sound-vibrations do not exactly follow the laws of the pendulum, and diverge from them in proportion as their amplitude of vibration is greater.

He further calculated that there must be a second *combination tone*, which must be higher than the two primary tones, to which he gave the name of *summational tone*, because it results from the sum of their vibrations. He assumed that the summational tone must be far more difficult to distinguish than the differential tone, because it is weaker, and that it can only be detected when the primary tones are very loud, and the ear brought close to the organ-pipe used as the sounding instrument. It must be said, however, that many physicists and physiologists with a keen and well-trained ear are unable to perceive the summational tone of Helmholtz. Righi is inclined to regard the summational tone as a purely theoretical mathematical deduction.

XI. We must now return to the main problem in the physiology of audition—namely, the mechanism by which the more or less compound tones give rise in the organ of Corti to neural excitations, which in consciousness assume the form of auditory perceptions, with all their various quantitative and qualitative characters. To appreciate the difficulty of solving this psycho-physical problem, it is necessary to remember that our auditory apparatus is capable not only of perceiving fundamental tones and sounds, but also of analysing and distinguishing the separate elementary components of the most complex vibrations, which result from the algebraic sum of a great number of coincident tones and sounds.

Space forbids us to enter into the various and imperfect theories put forward in explanation of the phenomena of hearing; we can only investigate those which, however incomplete and inadequate, have found wide acceptance, because they agree best with the general principles of psycho-physics.

From 1877 to quite recent times the illustrious name of Helmholtz fathered an ingenious theory of audition, which was based on the law of resonance and the extension of Johannes Müller's law of specific energy to the separate fibres of the auditory nerve.

According to Helmholtz it is impossible that excitation of one and the same fibre of the auditory nerve can give rise in consciousness to sensations of tones of different pitch. Seeing that, so far as we know, the stimulation of a nerve invariably produces the same effect, whatever the stimulus that arouses it, and that the quality of the effect remains the same, whatever the rhythm of the stimulation, it follows—according to Helmholtz—that one and the same fibre of the auditory nerve cannot respond to tones of different pitch, but must always evoke the sensation of a tone of uniform pitch. So that to explain the faculty by which the ear perceives different notes of the musical scale it is necessary to extend the law of specific energy to the component fibres of the cochlear nerve, and to assume that the

organ of Corti is provided with as many specifically differentiated nerve-fibres as there are perceptible tones. This qualitative difference in the fibres of the acoustic nerve, which is one of the postulates of Helmholtz' theory, presents a certain analogy to the difference in the sensations aroused by the tactile nerves in different parts of the skin, in so far as these can be distinguished by their *local signs.*

A simpler hypothesis to explain the ability of the ear to distinguish different tones is that which assumes that each tone of any given number of vibrations, which agitates the fluid of the labyrinth, simultaneously excites all the fibres of the auditory nerve, and that the pitch of the note is distinguished in the brain by the number of the waves carried to it by the nerve in the time-unit. But when we remember that, on Bernstein's computation, the duration of the nerve-wave is usually at least 0·0006 secs., and that, on the other hand, the number of perceptible tones may amount to 40·000 or 50·000 per sec., this assumption appears extremely improbable—little less so than the hypothesis that we distinguish colours by the number of the nerve-waves transmitted to the brain by the fibres of the optic nerve.

To explain the mechanism by which single tones are capable of separately exciting one or a few specifically different fibres of the acoustic nerve, Helmholtz assumed that the organ of Corti is a graduated system of resonators capable of vibrating to the different tones of the scale. This theory was repeatedly advanced before the time of Helmholtz. To cite one name, Cotugno, in an anatomical treatise on the ear (Naples, 1760), compared the cochlea to a lute, and held that the perception of the higher tones depends on the lower spirals, and that of the lower tones on the apical convolution. Helmholtz, from similar anatomical considerations, urged the same hypothesis in a most striking manner when he compared the organ of Corti to a piano.

Starting from the non-homogeneous structure of the basilar membrane, and specially from the fact that it has a continuous series of elastic fibres stretched in a radial direction, which increase in length twelvefold as they ascend from base to apex of the cochlea, and are connected by a membrane which is longitudinally but little distensible and easily lacerated, Helmholtz imagined that these radial fibres might represent a system of strings, similar to those of a piano—tuned and capable of vibrating with the different notes of the scale. The wonderful faculty of the ear for analysing complex tones would depend on the fact that each radial fibre of the basilar membrane can vibrate to a given tone, so that when a complex vibration is transmitted to the cochlea the partial tones of which the sound is composed throw separate fibres into vibration, and these excite distinct nerve filaments, which are specifically differentiated at the

periphery as at the central end. The same occurs in a pianoforte when the dampers are raised. If the sound-wave of a powerful note is directed against the strings by a musical instrument or by the human voice, all, and only, those strings vibrate simultaneously of which the tones are contained in the note sounded. If, writes Helmholtz, every string of a piano could be joined to a nerve-fibre so as to throw it into excitation, each sound produced by the instrument would (as is the case in the ear) call forth a series of sensations exactly corresponding to the pendular vibrations into which the original movement of the air was decomposed, and the presence of each of the constituent harmonies would be perceived in exactly the same way as in the ear.

Numerous objections can be raised to this inviting theory.

We have seen that the membrane of the organ of Corti which can vibrate most easily is not the *basilar*, but the *tectorial* membrane, which is normally stretched over the end of the filaments of the hair-cells. The extreme shortness of the elastic radial fibres of the basilar membrane (fractions of a millimetre) makes it inconceivable that they can be tuned and capable of vibrating to the different notes of the musical scale, particularly to the lowest notes—which require very long, thick strings. On the other hand, even if we admit that the number of radial fibres in the basilar membrane is sufficient to fulfil the requirements of this theory, it is highly improbable that there can be a corresponding number of specifically differentiated nerve-fibres. Granting, with Helmholtz, that 4200 resonators are enough to cover the seven octaves used in music and another 300 resonators the other extreme, non-musical tones, the organ of Corti must as a whole comprise 4500 distinct resonators, with as many specifically differentiated nerve-fibres and central organs!

Another objection arises from the fact that the basilar membrane is in reality not a system of radially stretched strings, but a continuous membrane, the elements of which are not suited to receive the waves corresponding to the respective notes, and to transmit the separate impulses they excite to the brain. The vibrations of any element of such a membrane must, no matter how weakened they may become, be transmitted to the other elements. Even when any given tone impinges on a series of resonators, not only are those corresponding to it thrown into vibration, but those in which the vibration-number differs only slightly from that of the given tone vibrate as well.

Finally, Helmholtz' theory encounters grave objections when it is considered from the phylogenetic standpoint. The excessively numerous specific differentiations of the fibres of the auditory nerve demanded on the resonance theory, according to which a well-developed and perfectly trained ear is capable of perceiving all tones and sounds, could not have been developed simul-

taneously for the whole series of tones and sounds, but must have evolved gradually, beginning with such as are indispensable to the ear functioning as a resonator for the most ordinary sounds of its environment. This, however, conflicts with the uniformity with which the ear can appreciate all sounds within the limits of acoustic perception. Though every one recognises the fact that the ear becomes, musically, much more acute by practice, there are normally no gaps in audition within the scale of perceptible tones.

Notwithstanding these and other more or less serious objections to the theory of Helmholtz it undoubtedly affords a ready explanation of many acoustic phenomena, as well as of clinical and experimental observations, although they cannot be said to prove it directly.

The capacity of the ear for distinguishing the different qualities of tones, and the well-established fact (Hermann and Lindig) that dislocation of the phases of two simultaneous tones does not perceptibly alter *timbre*, even when it causes marked changes in the form of the complex waves that result, are readily explained by Helmholtz' theory, which assumes that the organ of hearing analyses the tones, and separately excites the single fibres corresponding to the component tones of which they are built up, independently of the form of the resulting waves.

By means of the resonance theory again it is easy to explain the phenomenon of *beats*, though the explanation of the origin of *Tartini's tones* in the same way is more difficult. In fact the latter cannot be accounted for at all, if we admit with Lagrange and Young that they are subjective interference phenomena, because, as such, it is impossible to see how they can excite the corresponding resonators of the organ of Corti. Helmholtz endeavoured to prove their objective existence, and the more recent work of K. Schäfer and Zwaardemaker is in favour of this view.

We have said that normally there are no true auditory lacunae in the scale of perceptible tones. Bezold, however, by means of a contrivance which enabled him to vary the pitch of tones from the highest to the lowest without interrupting the sequence, found that in different individuals larger or smaller gaps occur at the extremes of the series of perceptible tones. Some people show a defect at the upper and lower ends of the tone-range, others only at the lower, or only at the upper, auditory limit. In these cases there is a more or less considerable restriction of perception at the ends of the scale, that is, a diminished range of sensibility to tones rather than a hiatus.

But there are a number of otological observations, particularly on deaf-mutes, which show the presence of true lacunae of hearing, in other words of "acoustic islands." Some individuals are unable

to perceive single tones or groups of neighbouring tones, while they preserve the perception of other notes of the scale, which form, as it were, auditory islands contiguous to the lacunae. This can be readily explained by the resonance theory, assuming circumscribed and disseminated lesions in the organ of Corti, owing to which the function of certain elements on which depend the perception of certain separate notes or groups of notes is abolished.

It is more difficult to explain by Helmholtz' theory the clinical cases of continuous, subjective sensations of special tones (Stumpf), and cases of what is known as *double disharmonic hearing* (Jacobson). In the latter affection patients have a wrong perception of certain notes in the affected ear, or of a more or less extensive portion of the musical scale, so that combined hearing with the healthy and the diseased ear gives rise to disagreeable dissonances.

Helmholtz' theory that the perception of the highest tones depends on the first convolution of the cochlea, *i.e.* the part of the organ of Corti that lies nearest the fenestra ovalis, where the stapes is inserted, and of the deepest tones upon the apical spiral, *i.e.* nearer the helicotrema, is partially supported by anatomical observations in certain clinical cases. Moos and Steinbrügge, for instance, in sections from a patient who had lost the perception of high notes, found atrophy of nerve filaments in the first convolution of the cochlea. Other otologists, from their observations, arrived at conclusions contradictory to those of Helmholtz (Stepanow). Baginsky tried to solve the question experimentally, on dogs, by destroying the whole of the cochlea on one side, and its apex or base alone on the other. In the first case he found deafness to deep tones, as shown by their reactions, but in the second he was never able to prove deafness to high tones. These results were afterwards confirmed by R. Ewald. But they only partially agree with Helmholtz' theory, and may, as we shall see, be adequately explained by a perfectly different theory.

In conclusion it may be said that in proportion as the analysis of auditory phenomena becomes more complete, arguments accumulate which tend to disprove rather than to confirm the resonance theory. Hermann, Mach, König and others have all declared against it.

In 1886 Rutherford proposed a different theory of hearing, which is the logical development of a conception already put forward by Rinne (1865) and Voltolini (1885). According to Rutherford the mechanism by which the cochlear apparatus is excited is comparable with that of the telephone. The vibrations transmitted to the fluid in the scala tympani through Reissner's membrane impress the tectorial membrane and hairlets of the hair-cells. The hairlets are all excited simultaneously, and again

transmit the vibrations they receive to the respective nerve-fibres in corresponding frequency, amplitude, and form, just as in a telephone the sound-waves are transformed by the metal plate and magnet into electrical movements which correspond to the shocks which produce them.

According to Rutherford the analysis of tones takes place, not at the peripheral organs, but in the centres, and it is impossible to offer any mechanical explanation of it.

Rutherford's theory of the excitation of the organ of Corti as a whole, by means of sound-waves transmitted from the tympanic apparatus, presents obvious advantages over that of Helmholtz, and avoids the more serious objections to which the latter is open. But it has one grave defect, which almost entirely deprives it of the character and importance of a true theory of audition. It assumes that when stimulated by sound-waves the auditory nerve can transmit them to the brain, with all their characteristics of frequency, intensity, and timbre, as though the fibres which compose it were fully analogous to the metal wires of a telephone.

Rutherford endeavoured to justify his theory experimentally. When a motor nerve is excited by rapid shocks from an induced current there is complete tetanus of the muscle if the number of shocks is 40 per second, and with increased frequency of the stimulus the muscle remains in tetanus. But on auscultating the muscle by suitable means while it is in tetanus a sound is heard, according to Rutherford, the pitch of which varies up to a certain point with the frequency of stimulation; this was demonstrated by Lovén, who considered the sound produced to be the effect of electrotonic variations in the nerve. When, for instance, 40 shocks per second are sent into the nerve a deep tone of 40 vibrations is heard. Rutherford found that on applying 352 stimuli per second there is a muscle-sound of corresponding pitch. At a still higher frequency of stimulation there is no longer any tone, but only a noise. This does not, according to Rutherford, invalidate his theory, because the muscle-fibre is quite different from the nerve-fibre or cell, which he believes capable of receiving stimuli of far higher frequency than these. He refers in this connection to the wings of insects, as bees, the motor nerves of which are capable of conveying to the muscles fully 460 impulses per second. But even this is far removed from the 40,000-50,000 vibrations of the highest perceptible tones.

Another very cogent objection which may be raised against all theories which, like Rutherford's, deny the peripheral analysis of tones, and refer this faculty to the cerebral cortex, is that they do not take into account the complex structure of the organ of Corti and the cochlea in general, when they ascribe to it the comparatively simple function of a vibrating membrane. Comparative

anatomy shows that in ascending the animal scale the cochlea becomes increasingly complex in all its parts, until in man it undoubtedly possesses a greater power of analysing tones than in any other animal.

To meet this objection A. D. Waller (1891) proposed an ingenious modification of Rutherford's theory by assuming the *basilar membrane* (or rather the entire organ of Corti) to represent a long, narrow membrane which takes up the complex vibrations of the membrana tympani and vibrates in its entire area to all sounds, although more or less in some parts than in others, according to the qualitative differences of the sonorous impulses that impinge on it. If we picture the function of the organ of Corti according to this interpretation, it seems, says Waller, to give "what we may designate as *acoustic pressure-patterns* between the membrana tectoria and the subjacent field of hair-cells. In place of an analysis by consonation of particular radial fibres it may be imagined that varying combinations of sound give varying pressure-patterns comparable to the varying retinal images of external objects." [1]

While on Rutherford's theory analysis of tones takes place not in the cochlea but in the brain, Waller holds that there must be a certain degree of peripheral analysis, by means of the different pressure-patterns produced by different tones and noises, although he still leaves their more complete and delicate analysis to the brain.

Another opponent of Helmholtz' theory was M. Meyer (1898), who also maintains that sound-analysis takes place in the organ of Corti by vibrations, not of single radial fibres, but of more or less extensive segments of the basilar membrane. The strength of the tone sensations would depend on the length of the vibrating segments, the pitch upon the frequency of vibration.

Ter-Kuile (1900) supported a similar view. He started from the fact that the base of the stapes at each incursion drives a certain amount of lymph along the scala vestibuli, and thus produces curvature of a portion of the basilar membrane proportional in length to the period of the vibration, *i.e.* the depth of the tone. So that the length of basilar membrane incurved would form the measure of pitch. Each harmonic that accompanies the deepest tones would cause a change in the modality of the total excitation of the nervous apparatus, to which is due the central perception of *timbre*. Ter-Kuile's theory does not sufficiently account for the perfect analysis of compound sonorous vibrations into the separate components in the cochlea.

These incomplete and rudimentary theories of hearing put forward by Waller, Meyer, and ter-Kuile are interesting as precursors of the new theory proposed by R. Ewald (1899–1903).

[1] *Human Physiology*, Waller, 3rd ed. p. 474.

Ewald starts from Waller's theory that single tones may imprint different pressure-patterns upon the organ of Corti, comparable with the images on the retina. Every tone that impinges on the ear causes the basilar membrane to vibrate in its entire length, since it subdivides into a series of stationary waves of definite form, constituting as a whole what Ewald terms "acoustic images," which produce perceptions of sound in the brain by means of the fibres of the auditory nerve. On Ewald's theory a different acoustic image, consisting of a series of stationary waves, corresponds to each tone. When several tones impress the organ of Corti simultaneously there occurs a superposition, but no change in the length of the respective waves, so that each of the acoustic images can be recognised. In this way peripheral analysis of the tones becomes possible. When the sonorous vibrations are a-periodic, so that the waves impinging on the basilar membrane are not stationary but mobile, noises instead of tones are perceived.



FIG. 95.—Small plate of aluminium, with Ewald's vibrating membrane in the centre (natural size).

Ewald gave his theory an experimental basis. If a rubber membrane, 15 cm. long and 6 wide, is stretched over a frame and

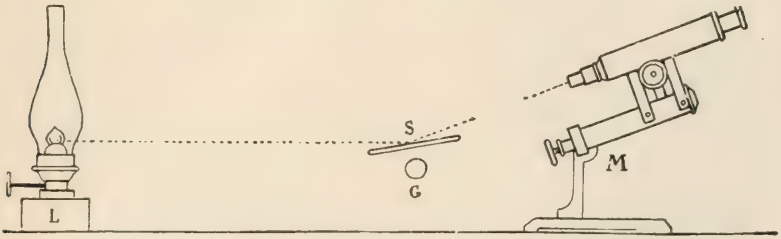


FIG. 96.—To show how Ewald's auditory images can be observed by the microscope on the vibrating membrane.

the surface smeared with oil to make it shine, a series of stationary waves (an acoustic image) appears on it when a tuning-fork is made to vibrate in its neighbourhood. These images vary perceptibly if the note of the tuning-fork is altered.

In order to reproduce the peculiar characteristics of the vibrating apparatus of the internal ear as exactly as possible Ewald (1903) prepared a delicate membrane, 8·5 mm. long and 0·55 mm. wide (Fig. 95). On this membrane, which he takes as the counterpart of the basilar membrane, different sonorous images, corresponding to the notes of certain octaves, can be observed with the microscope (see diagram of Fig. 96). The lowest tone capable, according to Ewald, of producing a visible image on this membrane is *B* of the small octave (= 247·5 *d.v.*), and the highest is a_4 (= 3520 *d.v.*). It remains to be seen whether further technical

developments of the method will make it possible to represent the lowest and highest perceptible notes in specific sound-images.

Ewald's acoustic images can be photographed like any other microscopic image, since they consist of a series of stationary waves. Fig. 97 shows a specimen of these photographs; it represents the most central part of the series of waves that extend over the whole length of the membrane. As the waves can only be seen and photographed when the membrane is viewed obliquely, the regular form of the wave is obtained only in the centre of the figure, which corresponds to the focus of the microscope.

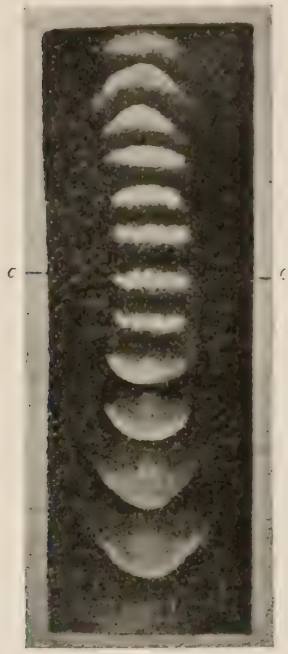


Fig. 97.—Photograph of the auditory image of a tone obtained with the membrane shown in Fig. 95.

The acoustic images are obtained not only when the different musical notes are produced by a Galton whistle near the membrane, but also when it is immersed in water, under conditions which schematically reproduce those of the inner ear. Ewald constructed a *camera acoustica* which represents a model of the auditory apparatus, as G. B. Porta's *camera obscura* is a model of the visual apparatus (Figs. 98, 99).

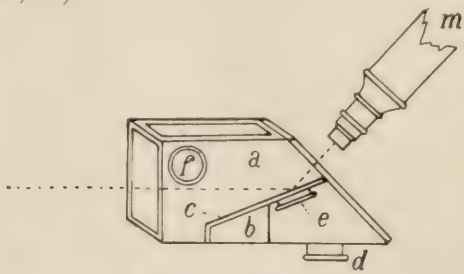


Fig. 98. Ewald's camera acoustica. Explanation in text.

Ewald constructs the elastic membrane for the reproduction of the stationary waves as follows. In an aluminium disc 0·075 mm. thick he cuts a rectangular slit with sharp, smooth edges (Fig. 95). He then plunges the disc by means of forceps into a solution of india-rubber and benzene (1 grm. non-vulcanised rubber in 20 cc. benzene) and withdraws it rapidly. After removing the excess solution from the edges of the disc he dries the thin layer of fluid which covers the slit in the disc, by waving it gently in the air, taking care that the delicate membrane is of uniform thickness throughout. It is only under these conditions that the membrane can be utilised for observation of Ewald's stationary waves.

His camera acoustica consists of a chamber, entirely filled with water, and divided inside by a partition (*c* of Fig. 98) which can be drawn out, and holds the capsule *e* in which is the aluminium disc with the elastic membrane. The stationary waves produced upon this membrane are observed in the microscope, illuminated through the glass walls of the chamber.

The interior of the chamber is thus divided into two portions by the partition wall *c*: the anterior chamber *a*, and posterior chamber *b*, corresponding with the scala vestibuli and scala tympani. In the wall of the anterior chamber *a* there is a hole *f* which corresponds with the fenestra ovalis, and is covered with a rubber membrane.

A similar hole *d*, also covered with a rubber membrane, is made in the floor of the posterior chamber, which represents the fenestra rotunda. Pressure upon the membrane of the fenestra ovalis causes that of the fenestra rotunda to bulge out, and the little elastic membrane of the aluminium disc is necessarily displaced in the same direction.

The camera acoustica is fixed horizontally by the metal support *c* and screw *b* to the pillar *a* (Fig. 99). It is then connected with a simple contrivance for the transmission of sound-waves, which is attached to the pillar *f*, and consists of a receiving funnel *e*, closed at the bottom by an elastic membrane (the tympanum); this is connected with the fenestra ovalis by

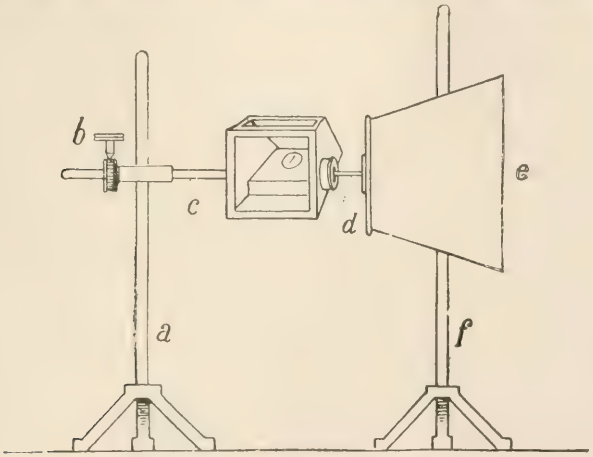


FIG. 99.—Ewald's camera acoustica. Explanation in text.

the iron rod *d*, which carries two little discs at its two ends (chain of auditory ossicles).

When a note is whistled or otherwise sounded in front of the receiver, the sound, as in the ear, is first transmitted to the tympanum, then by means of the rod (the ossicles) to the fenestra ovalis. The vibrations then pass through the water of the chamber, and throw the elastic membrane into vibration. But here, too, as in the ear, it is possible for sound to be transmitted without the interposition of the rod. If the transmitting apparatus is removed, and the sound-waves are produced at a short distance from the fenestra ovalis, the stationary waves will equally be visible upon the membrane. And if a vibrating tuning-fork is placed directly upon one of the walls of the chamber, an acoustic image is formed (bone conduction).

Ewald's theory, unlike all other theories of audition (including that of Helmholtz), is based, not on purely hypothetical considerations, but on a physical fact which can be experimentally established by a model which adequately reproduces the fundamental conditions under which the auditory apparatus acts. He formulates the fundamental principle of his theory as follows:

"The impulses aroused in the ear by sound impress a wave-image upon the basilar membrane, the special form of which enables the basilar membrane to act as a link in the chain of the conducting apparatus, which is intermediary between the sound and the auditory sensation."

The facts on which Ewald bases his theory signify a real, positive progress in the difficult problem of audition. We would make only one objection, with reference to the mechanism by which he conceives the transformation of acoustic images into the psycho-physical process of neural excitation and auditory sensation. From what was said above of the structure of the organ of Corti (p. 219) it seems to us fully proved that the true vibrating membrane is not the basilar, which supports the epithelial cells of the peripheral organ of hearing, but the tectorial, which rests on the ends of the filaments of the hair-cells, and by displacement of the hairs excites the nerve-fibres with which these cells are richly provided.



FIG. 100. Ciliated nerve-cells of auditory neuro-epithelium of rabbit. (After Kolmer.) 1, basal membrane, passing through which the nerve-fibres lose their medullated sheath; 2, medullated fibre. The fibrils divide into two smaller bundles, each of which goes to form a network in two distinct hair-cells. The filaments of the hair-cells are not shown.

Kolmer's recent observations (1905) on the peripheral connection of the fibres of the cochlear nerve with the ciliated hair-cells of the rabbit bring fresh evidence in support of this theory, and show conclusively that Corti's hair-cells are true sensory nerve-cells.

As seen in Fig. 100, the fibres of the cochlear nerve that are distributed in the auditory neuro-epithelium of the rabbit lose their medullated sheath in passing through the basal membrane, and then arborise in the ciliated cells. One single fibre may, by branching, supply two separate hair-cells —which directly refutes the theory of Helmholtz. The neuro-fibrils of the axon on reaching the base of the hair-cell penetrate into it and form a network with narrow meshes towards the summit of the cell, which, however, they never reach. Kolmer's demonstration gives histological evidence of the theory that the filaments of the hair-cells, which we may conceive to be endowed with exquisite sensibility, are the intermediary through which the vibrations of the tectorial membrane give rise to excitations of the nerve-fibres which, on reaching the centres, arouse auditory sensations.

With this alteration and amplification, it appears as though Ewald's theory might successfully avoid all the objections to which that of Helmholtz is open.

By means of Ewald's theory it is possible to extend to auditory sensation the principle demonstrated by Mach for tactile and visual sensation, viz. that it is not necessary in explanation of the sensations of the different tones to consider the separate fibres or groups of fibres of the auditory nerve as specifically differentiated. They may all be identical *inter se*. The sensations of different tones depend on the spatial distribution of the peripheral excitation. It is the auditory image that characterises the tone, and this image is always well defined and easy to recognise, even when, owing to the absence of certain waves, it is interrupted or imperfect. These peripheral images caused by tones need not (as in Helmholtz' theory) have any absolute, but only a relative value. Only when they are a combination of different regular or irregular spatial periods do they assume definite significance in the sensory centres. The peripheral sound-images are only the *local signs*, which are perceived in our consciousness as tones of different pitch, strength, and *timbre*.

Consonance arises when the auditory images corresponding to two or more simultaneous tones are superposed and interposed in regular alternation. *Beats* or *intermittent tones* are produced when the rhythmical impulses required for the production of stationary waves are not all equal—so that rhythmical lacunae occur in the sound-images.

Ewald's theory explains our faculty of arranging tones in series according to their pitch. We judge the spatial differences between the sound-images as differences in tone. Different individuals are more or less musically gifted, according to their capacity of appreciating the different spatial relations between the manifold acoustic images formed simultaneously on the vibrating membrane of the organ of Corti. The ability to judge the relative value of two notes that approximate closely in the number of their vibrations depends on the power of estimating the minute spatial differences between the auditory images. Obviously this must vary considerably in different individuals.

Lastly, from the phylogenetic point of view, Ewald's theory makes it comprehensible how a gradual, uniform, general evolution of the whole apparatus of hearing was advantageous to future generations, whatever the specific acoustic circumstances of their environment.

The theory of acoustic images is also supported by the facts of pathology and experimental physiology. Deafness to deep tones when the apical convolution of the organ of Corti is affected in man, or artificially destroyed in the dog, is the natural consequence of the shortening of the acoustic scale at its lower end. On the other hand, pathology shows that deafness to high tones may be observed in cases of cochlear disease in which no segment

has been lost. These functional affections cannot be produced artificially by partial destruction of the basilar membrane of the cochlea, as would be the case according to Helmholtz' theory. They can readily be explained if we assume with Ewald that the vibratory power of the tectorial membrane is hindered in some way—as occurs experimentally, when his elastic membrane is imperfect.

The abnormal phenomenon of the so-called "acoustic lacunae" or "islands" was considered to be direct evidence for the resonance theory. But Ewald proves that it can be still more easily explained by his theory. He actually found that some of his artificial elastic membranes, of which certain portions were defective, showed lacunae in the series of stationary waves that arise when a tone is produced near them.

In conclusion, therefore, it may be said that although the theory of sound-images is still imperfect, it appears to meet all the principal objections made to the resonance theory.

XII. Having thus studied the mechanism by which the physical phenomenon of sonorous vibrations is transformed into the physiological excitation of the nerves and centres of hearing, we must briefly consider the *æsthetic* or *emotional* side of acoustic perceptions, on which the art of music is founded.

Music excites our emotions not only by melody, that is, the rhythmical succession of pleasing tones of varying duration, but also by harmony, that is, the simultaneous emission of a number of tones, chords, and intervals.

Melody is not governed by definite rules; it is a purely intuitive art, belonging to the region of imagination. Innate in man, it has gradually been evolved and perfected in historical times, in a varying degree in different races and individuals, and is only to a minimal extent founded on *onomatopoeia*—or the imitation of tones and sounds in nature. Harmony, on the contrary, is the foundation of the art of music: while it is the result of artistic experience, it is subject to the laws of acoustics which are its scientific foundation. The task of the physiologist is to determine the relations between the physical laws of sonorous vibrations and the aesthetic or emotional characteristics of auditory perceptions.

Starting from the note selected as the standard of the international pitch, $a = 435$ double vibrations, 870 single vibrations (Vol. III. p. 148), and counting up all the tones above and below this note that can be perceived by a musically trained ear, we obtain an extensive series of gradually rising or falling notes, each of which can be distinguished from the next higher or lower note. The next highest note to the standard is represented by 435·4 *d.v.*, and the next lowest by 434·6. The entire octave, *i.e.* the interval $c^1 - c^2$, is divisible into more than 1200 tones which

can be distinguished by the ear. The total number of single notes that can be perceived by the normal ear is thus very considerable.

But we have already seen that in music the extreme perceptible tones, whether the highest or the lowest, are not utilised, so that the musical tone-range does not usually exceed seven octaves, commonly known as the contra-octave, great octave, small octave, once-, twice-, thrice-, and four-times accented octaves. Moreover, the very small intervals that can be distinguished by a good ear between two adjacent notes are not counted as true musical tones, these being confined to intervals of which the vibrations stand to each other in a given ratio. Thus, the once accented octave, which lies in the centre of the tone-range, is divided, not into 1200 tones, but only into 12, the least interval recognised between them being a *semitone*. The same applies to the octaves above and below. Intervals of less than a semitone are used in oriental vocal music, but in our system of music, when we do not employ instruments with the tempered scale (*infra*), we only make use of the so-called *enharmonic comma*, for which, however, there is no specific notation.

The most important musical intervals are the octave, in which the ratio of the vibrations of the two notes is as 1 : 2; the fifth, 2 : 3; the fourth, 3 : 4; the major third, 4 : 5; the minor third, 5 : 6; the major sixth, 3 : 5; the minor sixth, 5 : 8; the second, 8 : 9; the seventh, 8 : 15. To a musical ear these can always be distinguished from other intervals, whatever their position on the scale, so long as they are not at the extreme upper or lower end of the appreciable tones: their value, however, is not absolute, but relative.

From these intervals is derived the natural musical scale:—

$$\begin{array}{c} 24 : 27 : 30 : 32 : 36 : 40 : 45 : 48 \\ \mathrm{c} : \mathrm{d} : \mathrm{e} : \mathrm{f} : \mathrm{g} : \mathrm{a} : \mathrm{b} : \mathrm{c^1} \\ 1 : \frac{9}{8} : \frac{5}{4} : \frac{4}{3} : \frac{3}{2} : \frac{5}{3} : \frac{15}{8} : 2 \end{array}$$

The scale is continued above and below in the other octaves, the same intervals being repeated (Fig. 101). Between each two notes of this scale (C major), however, there is a semitone only between *e* and *f*, and between *b* and *c*. Semitones are obtained by adding to the notes the chromatic intervals of sharps and flats, *i.e.* notes higher or lower than those named in the ratio of about 25 : 24. *C* sharp has $\frac{25}{24}$ of the vibrations of *c*; *d* flat $\frac{25}{24}$ of *d*.

Clearly the single intervals between one note and the next are not absolutely identical; for instance, the interval between *c* and *d* in the scale of C major is not perfectly identical with that between *d* and *e*, although both are intervals of a whole tone. For while *d* represents $\frac{9}{8}$ of the vibrations of *c*, *e* does not exactly

correspond to $\frac{9}{8}$ of *d*. In harmony it is, however, necessary to be able to begin the scale on any note desired, giving it the value of the keynote, or *tonic*, and the octave has therefore been divided into twelve intervals of perfectly equal semitones (in the ratio of 1·05946 to 1): so that all the intervals except the octave have to



FIG. 101.—The upper figure shows part of the keys of a piano or harmonium with the symbols for notes used in Germany; the lower, the single notes corresponding to the white keys (scale of C major) in the key of the violin or double bass, with the international nomenclature. (Roiti.)

be slightly altered. This is the *tempered* scale followed by all instruments with fixed notes (pianoforte, organ, flute, etc.) and by the orchestra in general, while the former is the so-called *natural* scale. The following table brings out the differences in the two scales:—

Note.	Scale.	
	Natural.	Tempered.
c	1	1
d	$\frac{9}{8}$ = 1·125	1·12246
e	$\frac{5}{4}$ = 1·25	1·25992
f	$\frac{4}{3}$ = 1·333	1·33484
g	$\frac{3}{2}$ = 1·5	1·49831
a	$\frac{5}{3}$ = 1·666	1·68179
b	$\frac{15}{8}$ = 1·875	1·88775
c'	2	2

"The force of education and of habit is so great," writes Roiti, "that musicians usually follow the tempered scale, even in singing without accompaniment. But well-established experiments have proved beyond a doubt that in celebrated string quartets the great performers (using instruments without fixed notes) play by ear alone, and follow the natural scale, which science did not invent, but has only discovered."

In music, the intervals between two notes given out simul-

taneously are known as concords or discords, according to whether they produce agreeable or disagreeable sensations—which varies with different races, and also in different epochs and individuals. The musical theory of the Greeks was acquainted through the Pythagorean School, perhaps even through the ancient Egyptians, with the distinction of intervals into *symphonic* and *diaphonic*, which corresponded to concords and discords. They held the octave and the fifth to be symphonic; all the rest—including the third—to be diaphonic. In the Middle Ages the major and minor third and the sixth were added to the symphonic intervals or concords, and in the year 900 the fourth as well, though later on it was once more relegated to the discords. Modern musicians arrange the series of musical intervals commonly employed, according to the diminishing degree of consonance, as follows: octave, fifth, fourth, major third, major sixth, minor third, minor sixth.

Helmholtz was the first who attempted to give a strictly scientific explanation of the consonance and dissonance of intervals. For him a consonant interval is one that produces a uniform sensation of sound, a dissonant interval one that produces an intermittent sensation. Consonance relates to the affinity of tones, dissonance to the frequency of beats. Two fundamental tones are in greater affinity according to the greater number of partial tones they have in common. Consonance is greatest when the fundamentals of both tones are in the ratio of an octave, because in this case their partial tones are fused and the beats disappear. In examining the series of diminishing consonances, fifth, fourth, third, etc., the number of coincident harmonics is seen to decrease, while the possibility of beats increases. The diminution of consonance therefore goes parallel with the diminution of affinity.

This is plain from the following table, in which the relative number of the vibrations of the different tones of the scale and their corresponding harmonic partial tones is shown in series. The first row of figures for each interval represents the partial tones contained in the fundamental; the second, the partial tones of the second tone associated with the first. The partials of the two tones which coincide are given in black type.

Octave	1 : 2	**1**	.	**2**	.	3	.	**4**	.	5	.	**6**	.	7	.	**8**	.	9	. **10**
				2				**4**				**6**				**8**			**10**
Fifth	2 : 3	2	.	4	.	**6**	.	8	.	10	.	**12**	.	14	.	16	.	**18**	. 20
			3			**6**			9			**12**			15			**18**	
Fourth	3 : 4	**3**	.	6	.	9	.	**12**	.	15	.	18	.	21	.	**24**	.	27	. 30
			4		8			**12**			16		20			**24**			28
Major Third	4 : 5	4	.	8	.	12	.	16	.	**20**	.	24	.	28	.	32	.	36	. **40**
			5		10		15			**20**			25		30		35		**40**

Minor Third	5 : 6	5	. 10	. 15	. 20	. 25	. **30**	. 35	. 40	. 45	. 50									
			6		12		18		**30**			36		42		48				
Major Sixth	3 : 5	3	. 6	. 9	. 12	. **15**	. 18	. 21	. 24	. 27	. **30**									
			5			10		**15**		20		25				**30**				
Minor Sixth	5 : 8	5	. 10	. 15	. 20	. 25	. 30	. 35	. **40**	. 45	. 50									
			8			16	24			32			**40**		48					
Second	8 : 9	8	. 16	. 24	. 32	. 40	. 48	. 56	. 64	. **72**	. 80									
			9		18		27	36		45		54		63		**72**				
Seventh	8 : 15	8	. 16	. 24	. 32	. 40	. 48	. 56	. 64	. 72	. 80									
			15			**30**			45				60			75				

Certain not inconsiderable objections can be made to Helmholtz' theory of consonance and dissonance. To the idea that consonance results from a continuous and dissonance from an intermittent sensation, C. Stumpf (1898) objected that when the octave and fifth are produced with a tremolo they are converted into intermittent but not into dissonant intervals. Consequently there is intermittence without dissonance. On the other hand, there can be dissonance without intermittence. A tuning-fork of 500 double vibrations makes a discord with another of 700, or this again with one of 1000, without the slightest perceptible beat. Lastly, Stumpf noted that beats may occur with consonant intervals, which do not therefore become dissonant, and that on varying the height of the intervals the nature of the beats that accompany the same interval varies, though the degree of dissonance is unaltered. The beats may influence the effect and pleasing character of an interval, but the discord does not depend upon them. Neither, according to Stumpf, is the coincidence of the partial tones of two simultaneous sounds of any importance as far as consonance is concerned. If this were admitted, then the degree of consonance of any interval would depend on *timbre*, which is contrary to musical experience.

Stumpf replaces Helmholtz' theory by another, which ignores both beats and coincidence of partial tones, and finds the cause of consonance and dissonance in the greater or lesser fusion of the two fundamental tones in the brain. By *fusion* Stumpf means the gradually varying and qualitatively uniform character that results from two simultaneous impressions of sound. The same psycho-physical phenomenon is common to other specific sensations. We saw, for instance, that a metallic taste results from the fusion of acid and sweet in certain proportions; we also saw that it is possible to procure a comparatively new olfactory sensation by the psychical fusion of two or more odours simultaneously applied to the mucous membrane. In auditory sensation the psychical fusion of two distinct, simultaneous acoustic impressions is, according to Stumpf, one of the most

ordinary and conspicuous phenomena—it happens each time two simultaneous tones are appreciated as a consonance. The greater or lesser degree of consonance in the different musical intervals depends upon their varying capacity for complete fusion. A well-trained musical ear is always capable of analysing consonant intervals into their components; an unmusical or untrained ear is the less capable of such analysis in proportion as the consonance, that is the mental fusion, of the two component sensations is more perfect. Discords are the musical intervals that cannot be fused into a uniform sonorous perception, so that even an unmusical ear is capable of distinguishing the two simultaneous tones. Consonance is thus exclusively due to psychical fusion of the two component tones, and is, within the range of notes utilised in music, independent of the pitch and intensity of the partial tones that make up the interval.

The explanation of the fusion or non-fusion of tones, on which their consonance or dissonance depends, is a difficult psycho-physical problem, which has up to the present found no convincing or adequate solution. It may be assumed with Stumpf that when the numerical relation of the vibrations of the two simultaneous tones is comparatively simple two processes take place in the brain, which are more closely interrelated than when this relation is less simple. In the first case there is a specific relation between the two central processes; in the second, this relation is imperfect or absent. In the present state of our knowledge, however, it is impossible to define in what the supposed "specific relation" essentially consists.

Zambiasi (1903–1905) has recently formulated a new theory of consonance and dissonance which resembles that of Helmholtz in so far as it holds these phenomena to be dependent on physical, objective conditions of tone, independent of any central, psychical process; on the other hand, he adopted Stumpf's view that these phenomena depend essentially on the greater or lesser fusion of elementary sensations into a compound sensation of sound. For Zambiasi as for Stumpf consonance corresponds with complete, dissonance with incomplete fusion of several tones, but this fusion, according to Zambiasi, depends not on mental processes, but on a peripheral physical phenomenon, which consists in a new period, resulting from the combination of the vibrations of the two tones.

Just as the simple sensation of the pitch of the different elementary tones depends on the duration of the rhythmical vibrations, so the complex sensation that results from the combination of two simultaneous tones depends on the different duration of a new periodicity—distinct from that of the simple vibrations—formed in consequence of this combination. This is clear if we consider the physical significance of the relation between the number of vibrations of the two tones. When, *e.g.*,

we say that the ratio of the fifth is 3 : 2, this means that to every two vibrations in the fundamental tone there are three in the other tone, and that all these vibrations are necessary to make up the period of the interval. The two groups of vibrations, by fusing into a single period, arouse the complex sensation of the interval, whenever the duration of the new period differs from that of the periods of the two component tones, and is short enough to be comprised within the limits of tone-perception.

The special periodicity of the intervals at once becomes perceptible if we substitute a corresponding optical for the acoustic phenomenon. The optic image of the intervals can be obtained both with parallel and with vertical combination of the vibrations of the two component tones. The second case is represented by Lissajou's figures.

Lissajou's sound-images are geometrical forms which result from the rectangular combination of the vibratory movements of two simultaneous tones, produced by a beam of light.

In order to obtain optic figures of musical intervals Zambiasi used two tuning-forks, the tones of which formed definite intervals. To the end of one prong of the deep fork he attached a small aluminium plate with a hole in it, balancing the other prong by an equivalent weight ; to the end of the high fork he attached the lens of a microscope. With the illuminating apparatus of the microscope he concentrated an intense beam of light upon the little hole of the first fork, and projected the image of the hole upon a screen with the lens of the second fork.

The two forks were so placed — one vertical, the other horizontal — that they vibrated in planes perpendicular to the direction of the beam of light. The first fork in vibrating gave the image of a horizontal band of light upon the stationary screen, the second that of a vertical band. When both forks vibrated simultaneously Lissajou's figure, corresponding with the vertical coincidence of their vibratory movements, was produced. In order to photograph these figures Zambiasi substituted a sensitive plate for the screen, and placed it in a camera without a lens, using the lens of the second tuning-fork as the objective. In order to regulate the exposure as desired, a rotatory shutter is introduced which can be turned at the required speed.

To make Lissajou's figures mobile, so that instead of coinciding they fall one after another in successive phases upon a plane, Zambiasi substituted a frame for the screen, with a plane vertical to the direction of the beam of light, and allowed the carrier with the sensitive plate to pass at a uniform rate across the frame, so that the beam of light traced Lissajou's figure upon it.

Just as, on observing Lissajou's figures fixed on a stationary plate traced on a parallelogram, the number of vibrations of the two component tones can be recognised by the points of contact with two adjacent sides of the parallelogram, so on studying the tracings of these figures, as photographed by Zambiasi on his moving plate, the periods of the intervals can be seen at a glance and their duration measured.

The curves of Fig. 102 represent the optic images of five intervals arranged in the order of decreasing consonance: unison, fifth, fourth, seventh, augmented fourth. On comparing the dura-

tion of the periods of these intervals it is plain that the shorter the period the greater is the consonance, the longer the period the greater is the dissonance. Unison is not really a musical interval, because the two component tones, since they have the same number of vibrations, do not produce any new periodicity different from that of the simple tones. Consonant intervals appear as such in consciousness, because their period is so short that they fuse into a single uniform sensation. Dissonant intervals, on the contrary, have periods as long as those of the tones which lie near the lower threshold of auditory perception. They cannot, therefore, fuse into a uniform and continuous impression, and they produce a discontinuous and intermittent sensation in consciousness, which makes the two component tones more easily recognisable. Zambiasi holds that the lower threshold of audition, both for simple sounds and for intervals, depends on the physiological time-constant of the ear, and that no continuous sensation of the same is possible unless the duration of their period is shorter than that of the sensation.

When we consider that the time required to produce an auditory sensation is about $\frac{1}{20}$th second we can understand that at least 20 vibrations per second are necessary to cause a uniform sensation, so that when the elementary sensation of a vibration ceases the sensation of the next vibration should begin without a pause. Beyond this minimum of vibrations per second the threshold of auditory sensation is passed.

Zambiasi shows by a number of experiments that the new periodicity and the new sensation which arise from the coincidence of two tones forming definite intervals come under the same limitations and the same laws that regulate the sensation of simple tones. In order that the interval may produce a continuous uniform sensation the periods must not be so long as to occur less often than 20 to the second, which number is, as we have seen, the threshold of auditory perception. Above this threshold, up to 100 and more periods per second, there are two superposed sensations, one of a continuous sensation of sound, the other of simple a-phonic vibrations. The major third, for example, is hardly perceptible when the lowest tone contains 80 vibrations. This phenomenon is easily explained if we remember that the duration of its period is four times as great as that of the lowest tone, so that in this case the interval of the third has 20 periods per second, which is the physiological minimum for the perception of tones.

In polyphonic vocal and instrumental music it is not merely a question of sounding two instruments together, but of producing three or more tones simultaneously, which is commonly known as a *chord*. Chords, again, like simple intervals, may be consonant or dissonant, according as more or less fused and more or less

agreeable uniform perceptions are combined. But it cannot be denied that the euphony, the sweetness or harshness, of the chords are influenced not only by the degree of fusion, but also by the different quality and colour of the concurring tones and the

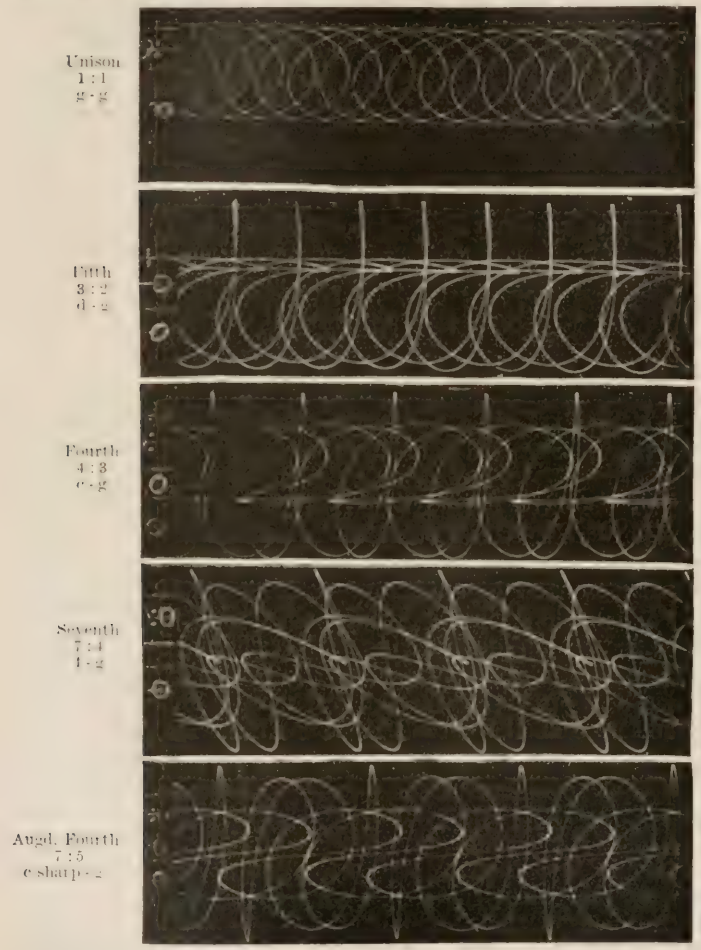


FIG. 102.—Optical images of five intervals arranged in order of decreasing consonance. (Zambiasi.) The vibrations of the two tones were combined vertically to obtain Lissajou's figures; these were traced by a luminous point on a sensitive plate moving uniformly at such a rate that the entire course of the curve was traced in one-tenth of a second. The tones were produced by the vibrations of two tuning-forks, one of which had a small aperture brightly illuminated by the sun, while the other had a lens through which the image of the slit was projected on to the photographic plate.

number of the resultant beats. It is thus easy to explain why the three notes, *c*, *e*, *g*, which are partial tones of one and the same fundamental note, and have no beats, form the most harmonious and perfect chord.

Musicians have for a long time distinguished between *major* chords and *minor* chords. In the former the three notes *c*, *e*, and *g* are the fundamental elements; in the latter, *c*, *e* flat, and *g*. These two chords give rise to quite different auditory perceptions, although the intervals remain the same and are merely displaced. In the major chord, *c*, *e*, *g*, the major third, *c*, *e*, precedes the minor third, *e*, *g*, while in the minor chord, *c*, *e* flat, *g*, the minor third, *c*, *e* flat, precedes the major third, *e* flat, *g*. It is difficult to define precisely in what the difference between these two chords consists, although the ear perceives it plainly. "The major chord," says Bernstein, "offers something clear, precise, and definite, and gives us the feeling of satisfaction, while the minor chord has an indefinite, vague character, which renders it appropriate to express melancholy."

According to Helmholtz the physical cause of the difference between major and minor chords lies in the ratio in which the resultant (differential) tones stand to each other. In major



FIG. 103.—To the left, Lissajou's figure of the perfect chord *do, mi, sol* (C, E, G), photographed on a stationary plate; to the right, the optical figure of the same chord taken on a moving plate. (Zambiasi.)

chords the resultant tones form a consonance, in minor chords a dissonance. According to Helmholtz it is this dissonance which gives to minor chords the contradictory indefinite character that renders them apt to express melancholy feelings. Assuming with Stumpf and Zambiasi that dissonance is caused by the imperfect fusion and length of period of the intervals, we may logically admit that the specific emotional character of minor chords is an effect of the same cause.

The hypothesis, according to which the degree of consonance of the intervals depends on the brevity of their periods, is also applicable to chords which consist of several tones. Musical chords are distinguished from the other infinite possible combinations of tones by having such a brief intrinsic period that they arouse a clear and continuous sensation. The fundamental chord *c*, *e*, *g*, for instance, is the combination of three tones which has the shortest possible period: it results from the combination of $4 + 5 + 6 = 15$ vibrations of the three tones, and the duration of its period is four times that of the vibration of the lowest tone (Fig. 103).

The most perfect fusion of tones is undoubtedly that of the harmonic particles from which vocal *timbre* is derived. In this case, however, the chord has no intrinsic period, but it is blended with that of the vibrations of the fundamental tone, which, by assimilating all the other tones, assumes a specific quality or colour.

Combinations of tones may therefore be classified as:—

(*a*) Chords which give *timbre*; this is the maximal degree of fusion.

(*b*) Musical chords with an intrinsic period, in which the fusion is not so complete that the component tones cannot be detected.

(*c*) Chords with very long periods, which give rise to no continuous or musical sensation.

XIII. We have said that little is known of the physico-chemical nature of the central processes that determine auditory perception. Minute analysis of these processes, however, reveals certain interesting peculiarities which we must briefly consider.

It has been fully demonstrated that both the recognition of pitch and the intensity of auditory sensations become more and more definite with each vibration. There is therefore a rising or waxing phase in auditory sensations, which conduces to the clear perception of their fundamental characters. We shall find the same in visual sensations.

Exner made a series of researches on the minimal number of vibrations necessary for the perception of tones, and proved that at least 16-20 vibrations must impress the ear before there can be a distinct recognition of pitch. At the same time he observed that the *C* of the great octave becomes clearer and more distinct with each successive vibration, and only attains its maximal degree of intensity after 44 vibrations; the *c* of the small octave reaches its maximum only after some 48 vibrations. These experiments tend to show that the intensity of tones increases rapidly at first and then more slowly, so that it is difficult to say at what moment it becomes maximal.

Similar researches were made by Max Meyer to show how the crude sensation of hearing passes gradually into the clear appreciation of pitch. He employed different sirens with 2, 3, 4, and 5 holes to determine the number of impulses required to perceive f^1. With only two impulses there is no recognisable tone; with three the sound begins to acquire a certain strength; with four the tone can be recognised, though it is still weak and obscure; with five the pitch is clearly appreciated. Urbantschitsch studied the same phenomena on both the healthy and diseased ear by employing the tones of tuning-forks of different strength. A very weak tone is only fully appreciable to a sound ear after

1-2 seconds of continuous impression. Persons who are partially deaf, or have disease of the middle ear, only perceive it much later. Many people can only hear a strongly vibrating tuning-fork or the ticking of a clock after 5, 8, or 10 seconds. Sometimes one ear hears before the other, so that in binaural hearing there is a kind of echo or sensation of a double sound. The eminent otologist Dennert (1899) showed the importance of these observations in testing audition. He used a vibrating tuning-fork which was rhythmically brought near or moved away from the ear of the patient, and proved that the less the aural acuteness and the feebler the tone, so much the greater must be the number of impulses which must summate in order to obtain complete perception.

The rising or waxing phase of auditory sensation (*Anklingen*) has its parallel in the falling or waning phase (*Abklingen*), which is due to the fact that the sensation continues for a certain time after the cessation of the physical vibration that produces it. Helmholtz took as the measure of this persistence of sensation the maximum rate at which two notes can be alternated in a trill, without fusion of the two consecutive sensations into one single sensation, as occurs with colours. The duration of the falling phase in hearing varies according to Meyer, Exner, and Mach with the pitch of the notes:—

For low notes (c^1) $= 0{\cdot}0395 - 0{\cdot}0209$ seconds.
„ high notes (c^4) $= 0{\cdot}055 - 0{\cdot}0008$ seconds.
„ noises $= 0{\cdot}016 - 0{\cdot}002$ seconds.

The persistence of the sensation on the cessation of the objective sound may be considered as an effect of imperfect damping of the vibrating parts of the ear, but it more probably depends on the persistence of the central nervous excitation, as has been demonstrated for other modalities of sensation.

Methods of investigating the Function of Audition.—Various methods are employed by otologists in investigating the hearing of patients. Whispering or—in cases of more severe affection—loud speaking is generally employed. The first ten numbers are usually pronounced at varying distances, and the patient repeats these if able to hear them. 18 metres is generally assumed to be the greatest distance at which a normal ear can still hear whispered words; but according to Malte a young man with normal hearing is able to hear them at 35-40 metres.

It must, however, be remembered that in using loud speaking or whispering as a test of auditory acuity the selection of the sound or word pronounced at a certain distance is not unimportant. The auditory distance varies within comparatively wide limits according to the sounds employed for testing, or more exactly the vowel on which the word-accent falls. As we have already seen (Vol. III. Chap. III.) single vowels, whether spoken or whispered, are pronounced with a progressively rising cadence (tone) in the series *u* (*oo*), *ó* (*or*), *ò* (*ol*), *a* (*ah*), *è* (*a*), *é* (*ē*), *i* (*ee*). It is therefore easy to draw up a table of two-syllable words embracing a series of sounds in which the accented vowel varies, as follows:—

For the vowel *u* (*oo*) = booty.
„ „ *ó* (*or*) = order.
„ „ *ò* (*ol*) = dollar.
„ „ *a* (*ah*) = father.
„ „ *è* (*a*) = lazy.
„ „ *é* (*ĕ*) = letter.
„ „ *i* (*ee*) = feeling.

Taking this scale as the measure of auditory acuteness, the words are audible at a progressively increasing distance in young people with normal hearing. According to Gradenigo the lesser distance for low sounds is more pronounced when the external and middle ear are affected than under normal conditions; in diseases of the labyrinth, on the contrary, audition of the higher sounds appears most defective.

Besides the human voice other sounds are used for testing audition, *e.g.* the ticking of a watch, or better Politzer's apparatus, consisting of a hammer which always drops from the same height upon a steel cylinder.

To test the perception of musical tones it is necessary to employ a series of tuning-forks, like that of Bezold and Edelmann, which extend from 12 to 870 double vibrations; for higher sounds an accurately graduated Galton's whistle, which can give 50,000 double vibrations, is now used almost exclusively.



FIG. 101. — Triangular pieces of black paper which can be applied to the prong of a tuning-fork.

In testing auditory acuity (*acumetry*) tuning-forks are used, and made to vibrate as far as possible at uniform intensity, while the time is measured during which the gradually diminishing sound is still perceptible. In practice this method encounters certain difficulties, owing particularly to the difficulty of determining time-relations in the decrement of tone. To obviate this difficulty Gradenigo (1899) proposed a new, easier and more exact method in order to obtain experimental proof of the diminution of sound from the tuning-fork. Starting from the fact that the intensity of a tone is directly proportional to the amplitude of vibration, he made the vibrations of one of the prongs of the fork which gave 40-60, at any rate less than 100, simple vibrations per second, visible to the eye, by fixing to its free end a triangular, elongated, black figure with sharp edges cut out of cardboard, bearing three or more divisional marks on one side (Fig. 104). Clearly, when the tuning-fork vibrates, the cardboard tongue must vibrate also, and produce a visual image which varies with the amplitude of vibration. At the maximum of amplitude, *i.e.* when the tone is strongest, two separate figures appear if the amplitude of the vibrations exceeds the breadth of the figure. When, as the tone diminishes, the vibrations become less ample, the two images begin to overlap at the inner side, and it is clear that the less the amplitude of vibration the larger will be the overlapping portion of the two images. The *intensity* of the tone made perceptible by this experiment is accurately estimated by the greater or lesser portion of the two images, which can easily be measured by the scale at the side of the figure (Fig. 105).

The note of the tuning-fork can be transmitted through the bone, as well as by the air. In Weber's test the stem of the vibrating instrument is placed on the middle line of the skull; in normal individuals the sound is then localised in the centre of the head, but if one ear is closed, or the external air-passage of one side blocked by disease, it is referred to this ear.

Rinne's test consists in the fact that in normal individuals the diminishing note of a tuning-fork, held close to the auditory meatus, is perceived for a longer time than if the fork is applied to the mastoid process; in other words, individuals with sound ears hear tones transmitted through the air

more clearly and acutely than those transmitted by bone-conduction. To this experiment it may be objected that the note of the prongs and that of the stem of a tuning-fork are not comparable, so that the tone of the stem only should be used.

Schwabach's experiment is based on the observation that when transmission of the sound-waves in the ordinary way is obstructed, the fork applied to the bone is heard somewhat longer than normally—only of course

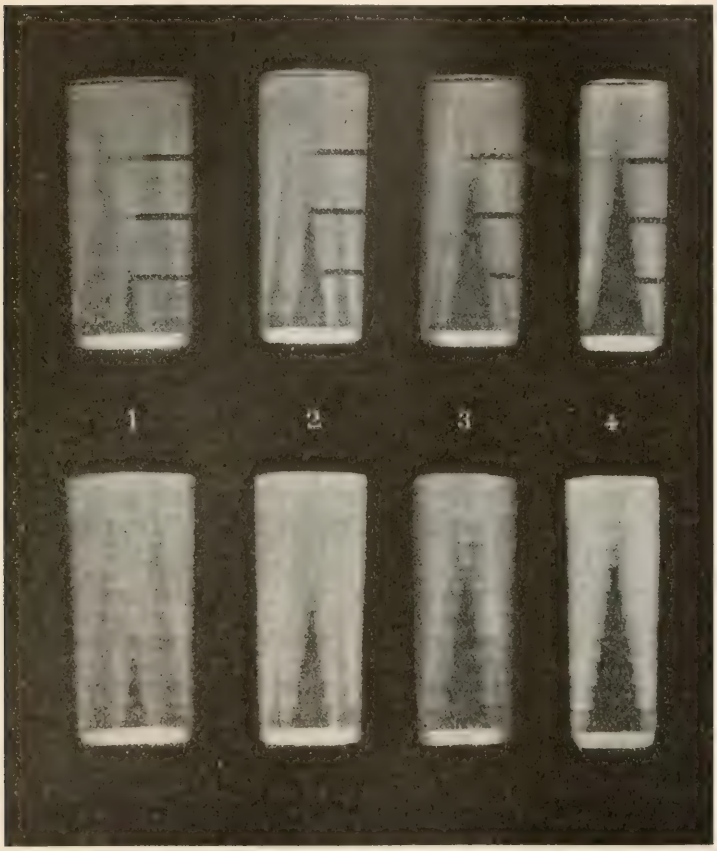


FIG. 105.—To show the changes in the optical images of the vibrations of a tuning-fork with gradual decrease in the amplitude of the vibrations. (Gradenigo.)

when the organ of Corti functions properly; if this be also diseased, the tone transmitted by the bones is heard with difficulty or not at all.

In Gellé's experiment air is blown artificially against the external auditory passage after the meatus has been hermetically sealed, until bone-conduction of the tones becomes weakened, owing probably to the pressure exerted on the organ of Corti by the tension of the tympanic membrane and the chain of ossicles. If the perception of sound thus conveyed through the bones is not weakened, it may be concluded that the articulation of the chain of ossicles (stapes) is anchylosed.

It is interesting at this point to consider the phenomena of *auditory fatigue*. In order to demonstrate that the peripheral and central neural apparatus of hearing can be fatigued, it is necessary to let a very powerful sound act on the ear for some time. The intensity of the sensation soon diminishes, and it may disappear altogether. According to Sylvanus Thompson (1881) there may also be the illusion that the source of sound is withdrawn farther and farther from the ear; in other words, owing to auditory fatigue, sound is falsely located. Similar results were obtained by Urbantschitsch (1881). He introduced two rubber tubes into the ears, the free ends being brought close to each other, so that the acuity of hearing in one or the other ear might be tested rapidly by the note of a tuning-fork. After convincing himself that both ears possessed the same degree of auditory acuity, he let a loud tone from a large tuning-fork act upon one ear for 10-15 seconds, and then damped the vibrations by placing his finger on the prongs till the tone became almost inaudible. As soon as the sensation ceased in the excited ear he quickly brought the fork close to the tube in the other ear, and observed that it was capable of perceiving the tone distinctly for several seconds, demonstrating fatigue of the ear first excited. This fatigue only lasted 2-5 seconds, after which time the fatigued ear again acted like the non-stimulated ear.

Another interesting experiment is reported by Tigerstedt. When the vibrations of a tuning-fork are transmitted from a distant room to both ears by a double telephone the tone perceived is localised in the median plane of the head. But if the tone is transmitted to one ear only, for a long enough time to fatigue it, and the second telephone is then applied to the other ear, the sound is no longer localised in the median plane, but on the side of the non-fatigued ear.

This very simple method not only demonstrates the phenomenon of auditory fatigue, but further brings out another interesting fact, namely, that fatigue does not influence the auditory acuteness for different notes of the scale, but only for that individual tone which produced it. When one ear is fatigued by one of the telephones with a tone, *e.g.*, of 360 double vibrations, and a tone of 365 double vibrations is then immediately made to act on both ears, no trace of fatigue can be discovered in the ear first stimulated, because the tone of 365 vibrations is localised in the median plane and not in the direction of the non-stimulated ear. Undeniably, this limitation of fatigue to individual tones that have affected the ear completely bears out Helmholtz' theory of resonators; but there is no proof that it cannot also be explained by Ewald's theory of auditory images.

Other phenomena in close relation with the function of the peripheral and central apparatus of hearing are *the entotic*

sensations and the subjective auditory sensations and hallucinations.

Entotic sensations are those which are caused, not by any external, but by an internal stimulus, which excites the peripheral auditory cells directly, or by transmission through the bones. Such are the rumbling noises heard when the external meatus is blocked by an accumulation of wax, or some foreign body, or when the Eustachian tube is closed by catarrh. They are explained by the fact that when the aerial transmission of tones and noises is hindered or prevented, the ear is hypersensitive to bone transmission, and perceives noises such as are caused by the circulation of the blood through the ear, the beating of the arteries, contraction of the muscles, and so on.

Subjective acoustic sensations do not depend on actual sound-vibrations, but on exaggerated excitability and the stimulation of the peripheral auditory apparatus by unknown factors. Some otologists distinguish these by the name of *labyrinthine acuphenes.* In character they generally resemble ringing, rushing or rustling, in which sometimes very high notes of the 3- and 4-times accented octave can be recognised, when the hyperaesthesia of the auditory cells is not evenly diffused over the whole organ of Corti, but more particularly involves special segments of it. These phenomena are common in anaemic, neurasthenic, and melancholic persons.

These simple subjective sensations must be distinguished from the persistent continuation and obstinate automatic and involuntary repetitions of notes, musical *motifs*, and verbal phrases, like a distant echo of something heard, which has made a particular impression on us. This often happens to people whose auditory sensibility is especially acute, after they have been to the theatre. These phenomena are essentially central in origin, and have the significance of a spontaneous revival of auditory memory images.

When the cerebral auditory images, which appear automatically, or perhaps in consequence of peripheral impulses which normally arouse entotic sensations only, are so vivid and prominent that they are projected outwards and confused with real acoustic images, they become *auditory hallucinations.* These are common in dreams, and their appearance in the waking state is a conspicuous symptom of different forms of psychopathy. According to their composition, auditory hallucinations are distinguished as *simple* and *complex.* These last may be disconnected and chaotic, or they may have a definite character, *e.g.* menacing or pleasant, and may be logically connected with complex psychical delirium. From the psycho-physiological point of view auditory hallucinations are of great importance as evidence that there is nothing in common between the sonorous vibrations of elastic bodies and the sensations of hearing, and that our

sensorial perceptions in general are not the reality, but are merely *images*, or *representative signs*, of reality.

XIV. The last point before us is to examine the functional importance or utility of *binaural audition* through which one ear is supplemented by the other, which makes the normal auditory function more perfect and complete, and facilitates judgment of the direction and distance of the source of the sounds that reach us.

G. B. Venturi, Professor of Physics at Modena, was the first who showed that our judgment of the direction of sounds is principally founded on binaural audition, and on the fact that one ear is almost always more strongly excited than the other. He set out his theory in a short Memoir (1802), and illustrated it by four convincing and well-established experiments:—

(*a*) If a blindfolded person, with one ear stopped and head motionless, is made to listen in the centre of an open space, free from all obstacles, to the tone of a flute, played at a distance of 14 or 15 metres, the sound is invariably perceived in the direction of the axis of audition, whatever the position of the person who plays the instrument. By "axis of audition" he means the line vertical to the median plane of the head or external surface of the ear.

(*b*) If the subject, instead of standing motionless in the centre of the space, turns slowly round on his own vertical axis, all other experimental conditions remaining unchanged, the tone he hears will be louder when the axis of audition of the open ear approximates to the direction of the sound-waves that reach the ear. Any one who is entirely or partially deaf of one ear has no other means of recognising the direction of a tone than by turning the head and observing how the intensity of the sound alters. But even then they often judge wrongly if the sound only lasts for a moment.

(*c*) If both ears are kept open and the subject still has his eyes blindfolded and his head motionless, he is capable of judging the direction of sound with tolerable accuracy, whatever the position of the player, at a distance of 14-15 metres. If the subject puts one finger into the left ear so as to close it gradually he receives the impression that the sound comes from another place, and approaches the axis of audition of the ear that was left open. If the other ear is then gradually unclosed the sound seems to go back to its original, and true, direction.

(*d*) With closed eyes, and both ears open, and the head motionless, the subject is unable to distinguish whether the sound comes from before or behind, when its source is in such a direction that both ears are stimulated with the same intensity. "So that it is from the inequality of the two simultaneous sensations of the two ears that we learn the true direction of sound."

These general conclusions of Venturi are borne out by all the scientific researches made later on with different methods.

Preyer, in a series of observations, endeavoured to bring the perception of the direction of sounds into relation with the orientation of the semicircular canals—a theory already propounded in Italy by Lussana. Münsterberg supported this view with certain variations. But since it has been proved that no auditory function can be assigned to the vestibular apparatus as a whole, the theory that the semicircular canals are responsible for the immediate sensation of the direction of sound has fallen through completely. On the other hand, v. Kries showed that the facts stated by Preyer and by Münsterberg may be explained quite simply by the different intensity of the sensations in the two ears—that is, by the old theory of Venturi.

Bloch, under the guidance of v. Kries, made a special study of the subject of binaural audition, and disposed of numerous errors that had accumulated. He found that in binaural hearing there was a reciprocal reinforcement of sensation, greater perhaps than would result from simple summation. With equal stimulation of both ears, the field of audition is projected to the middle of the head, with stimulation by tones of unequal intensity, to the side of the stronger stimulation.

The direction of the source of sound is determined as follows: The subject is blindfolded and placed in the centre of a circle with a radius of 1 metre; the circle is divided into 16 parts; at the middle of each part Politzer's *acumeter* is set going, and is then moved in one direction or the other along the periphery of the circle, while the subject is asked to judge the direction of the movement.

Bloch found that on moving the source of sound in front of or behind the subject variations of about 4·5 could be perceived. At the sides a displacement 6-7 times greater was necessary before the change could be recognised, no matter if the subject were standing or lying down. The same was the case for uniaural hearing, but the power of distinguishing the direction of displacement was much less. These results can be fully explained by differences in intensity of sensation, and partly also by the form of the external ear (pp. 195 *et seq.*). The proof of this lies in the fact that when the sound is produced in the sagittal plane the displacement must be about five times greater before it can be recognised.

The frequency of error in judging the distance of a sound seems to be in relation with the strength of the partial tones. It is usually an indirect estimation, based on the apparent intensity of tones, the absolute strength of which is known to us. Not only is binaural hearing of great importance to our judgment of the direction and the distance of the source of sound, but it

improves the auditory function, as Urbantschitsch showed experimentally. He conveyed the sound of the Neef's hammer of an induction coil to the ear by telephone. The position of the secondary coil at which the sound was not heard was taken as zero, and the rest of the scale was divided into 100 parts, from zero to the maximum intensity audible, when the following results (A, B, C, D) were obtained from four individuals:—

Pushing up the coil from zero:

	A	B	C	D
Right ear	10	6	8	55
Left ear	10	7	8	55
Both ears	5	3	5	51

This shows that binaural is much finer than uniaural hearing.

Tones and noises conducted by bone and not by the tympanic membrane are as a rule projected inwards and not outwards. This is observed under water, when the auditory passages are free from air (E. H. Weber). The note of a tuning-fork placed on the head is heard in the ear nearest to it. The limit of localisation for the two ears should correspond exactly with the median plane, but in practice this is rarely so, because the auditory acuteness of the two ears differs to some extent, even under normal conditions (Urbantschitsch).

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CHAPTER VI

DIOPTRIC MECHANISM OF THE EYE

CONTENTS.—1. General anatomy of eyeball. 2. Formation of retinal images; underlying optical principles. 3. Optic constants of the eye. 4. Static refraction of the eye (*emmetropia* and *ametropia*). 5. Refraction of the eye; mechanism and innervation of accommodation. 6. Far point and near point of clear vision; range and speed of accommodation. 7. Normal imperfections in the dioptric apparatus of the eye. 8. Dioptric importance of the iris. 9. Mechanism and innervation of pupil in accommodation; theory of pupil-reflexes. 10. Absorption and reflection of light in the eye; ophthalmoscopy and skiascopy. Bibliography.

HEARING and Vision are the two highest senses, the best developed and best differentiated both from the biological and from the psycho-physical standpoint. *Touch* only makes us aware of the existence of such bodies in the external world as come into direct contact with our skin; *hearing* only enables us to perceive sonorous vibrations at a variable distance; *vision* informs us of objects at vast, immeasurable distances, provided they give out, or reflect, light. While the adequate stimulus of auditory sensations consists in the vibrations of elastic bodies between relatively narrow limits of frequency and intensity, the adequate stimulus of visual sensations is represented by *light*, that is (according to physicists) by the vibrations of an imponderable medium, at a frequency of 480-760 trillions per second, while its wave-length is comprised between 700 and 430 $\mu\mu$ (millionths of a millimetre). These very rapid ethereal vibrations penetrate the transparent media of the eye and stimulate the sensitive terminal elements of the retina, and we are then, owing to the marvellous structure of the visual organ, able not only to recognise light and colour but also to estimate the form, size, position, and structure of the surrounding bodies.

I. Each eyeball is an elastic, almost spherical body. As a whole it constitutes the peripheral sense-organ of the optic nerve.

The earlier anatomists described the human eye as an organ composed of three concentric coats and three fluids. These were the *humor aqueus* (which still bears the same name), the *humor crystallina* (now known as the crystalline lens), and *humor vitreus* (vitreous body).

The outer or fibrous coat (known to the ancients indifferently as *sclera*, *cornea*, or *dura*) consists of two distinct parts: an anterior, transparent portion, the cornea, and a posterior, opaque part, the sclerotic. The middle coat, or uvea (from its likeness

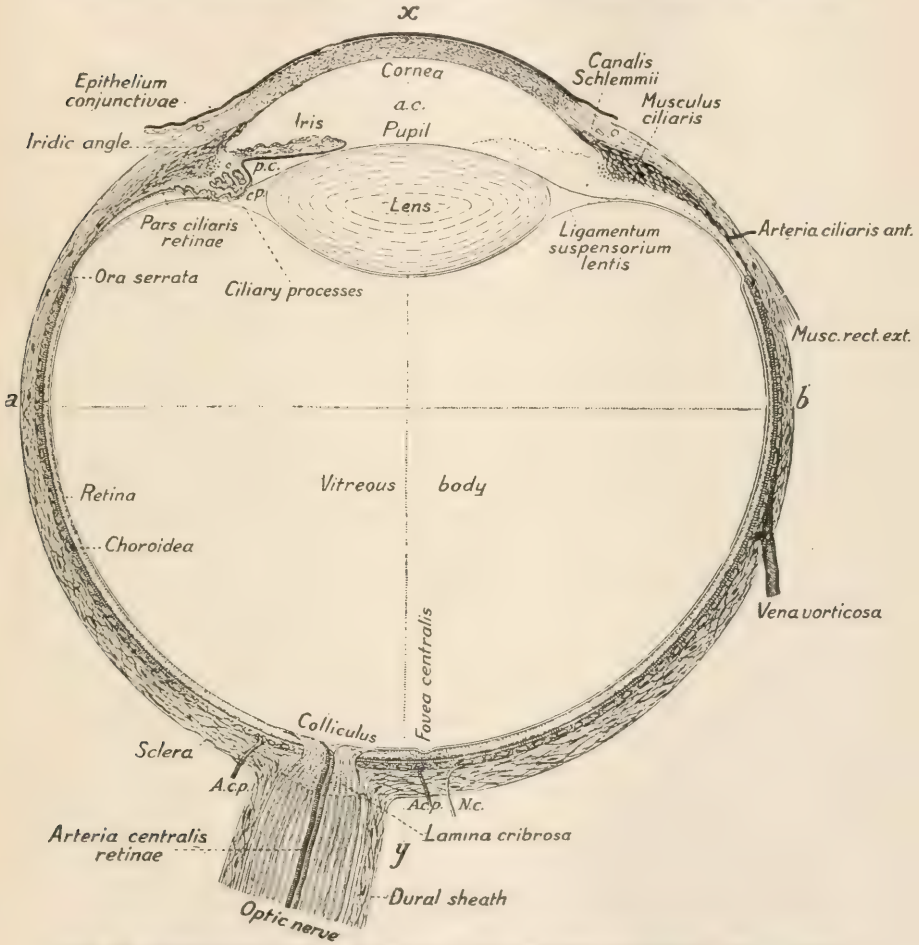


FIG. 106.—Diagram of the adult right human eye, horizontal section. Magnified 5 times. (Luciani from A. E. Schafer.) The line *a b* passes through the equator, *x y* through the optic axis of the eye; *A.c.p.*, posterior ciliary artery; *A.c.a.*, anterior ciliary artery; *N.c.*, one of the ciliary nerves; *V.v.*, vena vorticosa; *e.r.m.*, external rectus muscle; *a.c.*, anterior, *p.c.*, posterior chamber of the eye; *P.c.*, Petit's canal.

to a black grape from which the stalk has been torn away), is now subdivided into three portions—a posterior, pigmented part, the choroid; a middle region which is muscular and bears papillae, the zona ciliaris; and an anterior diaphragm formed by the iris, the aperture in its centre being the pupil. The inner coat, known as the retina, arachnea, or arachnoid, because it

resembles a spider's web, is subdivided into a posterior nervous part, the retina proper, and an anterior epithelial part, the pars ciliaris and pars iridica retinae (Fig. 106).

The outer coat serves in virtue of its fibrous character as the skeleton of the eyeball. In fact the motor muscles of the eye are attached to the outer surface of the sclera as the skeletal muscles are to the surface of the bones. In many animals the sclerotic has a tendency to ossify (birds, amphibia); the sclera of fishes contains large plates of cartilage. The curvature of the cornea forms the segment of a sphere of much shorter radius than that of the sclerotic. By analogy with the terrestrial sphere we speak of an axis, a meridian, and an equator in the eyeball; the line $x\ y$ of Fig. 106 is the geometrical axis of the eye, joining the anterior pole (mid-point of the cornea) with the posterior pole (point on the sclerotic lying somewhat externally to the entrance of the optic nerve). The line $a\ b$, joining two points of the maximal transverse diameter of the eye, passes through the equator of the eyeball. The line $x\ y$ is about 23·5 mm. long in the adult eye, the line $a\ b$ about 24·3 mm. long.

The anterior zone of the sclerotic, from about the line of attachment of the tendons of the recti muscles to the extreme edge of the cornea, is covered by the conjunctiva, which is reflected from the lids on to the eyeball, and is connected with the sclerotic by loose sub-conjunctival tissue.

The uvea is also known as the tunica vasculosa, from the great number of blood-vessels, united by connective tissue, of which it is made up. Its posterior portion or choroid coat and its middle or ciliary portion are applied to the inner surface of the sclerotic, with which they are united by means of a few filaments of connective tissue, vessels and nerves, which leave a small lymph space between the two coats, and enable the choroid to move on the sclerotic. The anterior portion of the uvea, the iris, is not in contact with the sclerotic, and the space between it and the cornea is known as the anterior chamber of the eye. Posteriorly the choroid is pierced by the optic nerve; and the centre of the iris is perforated by a circular aperture, the pupil. At the junction of the sclerotic and the cornea the uvea is firmly attached to the sclerotic by the ligamentum pectinatum.

The choroid is a brown membrane (black in most animals), which is soft, extensible, and easily lacerated. Three layers can be artificially distinguished in it: the external or lamina fusca, so called from the number of spindle-shaped or branched and more or less thickly pigmented connective-tissue cells that are scattered in it; the middle and thicker layer, consisting mainly of blood-vessels, but containing also a number of pigment cells, scattered in the interstitial spaces; the internal layer, represented by a hyaline membrane, which is transparent and elastic, and

is readily detached in macerated eyes (Fig. 107). On this elastic membrane—known as the membrana basilaris or membrane of Bruch—rest the hexagonal pigment cells, which form the tapetum nigrum and are in close morphological relation with the retina; these were for a long time erroneously held to belong to the internal layer of the choroid.

The ciliary portion of the uvea or zona ciliaris extends from the ora serrata to the pars iridica retinae. In the ciliary body the uvea becomes much thicker than in the posterior part of the choroid, owing to the appearance of two new formations, the ciliary muscle externally, and the corona of the ciliary processes internally.

The ciliary muscle is triangular in section. Owing to the direction of the smooth muscle-fibres of which it is made up it is usually regarded as two distinct muscles, an outer, consisting of fibres running in a meridional direction (Bruch's muscle, or

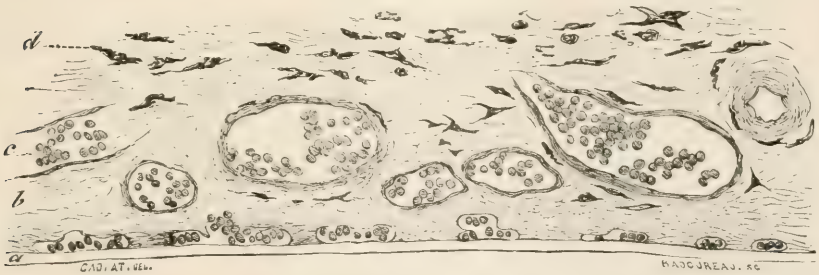


FIG. 107.—Section of choroid coat. (Cadiat.) *a*, membrana basilaris or membrane of Bruch; immediately above is the lamina chorio-capillaris; *b*, lamina vasculosa; *c*, vein with blood corpuscles; *d*, lamina supra-choroidea.

musculus tensor choroidae), and an inner, consisting of fibres forming a ring or sphincter round the insertion of the iris (Müller's muscle, or the circular ciliary muscle). Fig. 108 shows the fibres of the former in longitudinal, of the latter in transverse section. A third group of muscle-fibres run obliquely, interlacing so as to form a kind of network, their direction being intermediate between that of Bruch's and of Müller's muscles.

The ciliary processes, about seventy in number, form a circle of radial thickenings, which project into the anterior part of the vitreous humour (Fig. 109). They are free from the pigment which invests the remainder of the ciliary body, and contain a rich plexus of vessels, which anastomose and divide frequently. Between each two well-developed ciliary processes there are either smaller processes or an arteriole which runs direct to the iris.

The iris is a perforated membranous diaphragm placed in front of the crystalline lens, slightly convex towards the edge of the pupil and concave towards the periphery. The aperture of the pupil is not quite in the centre, but slightly inward. The

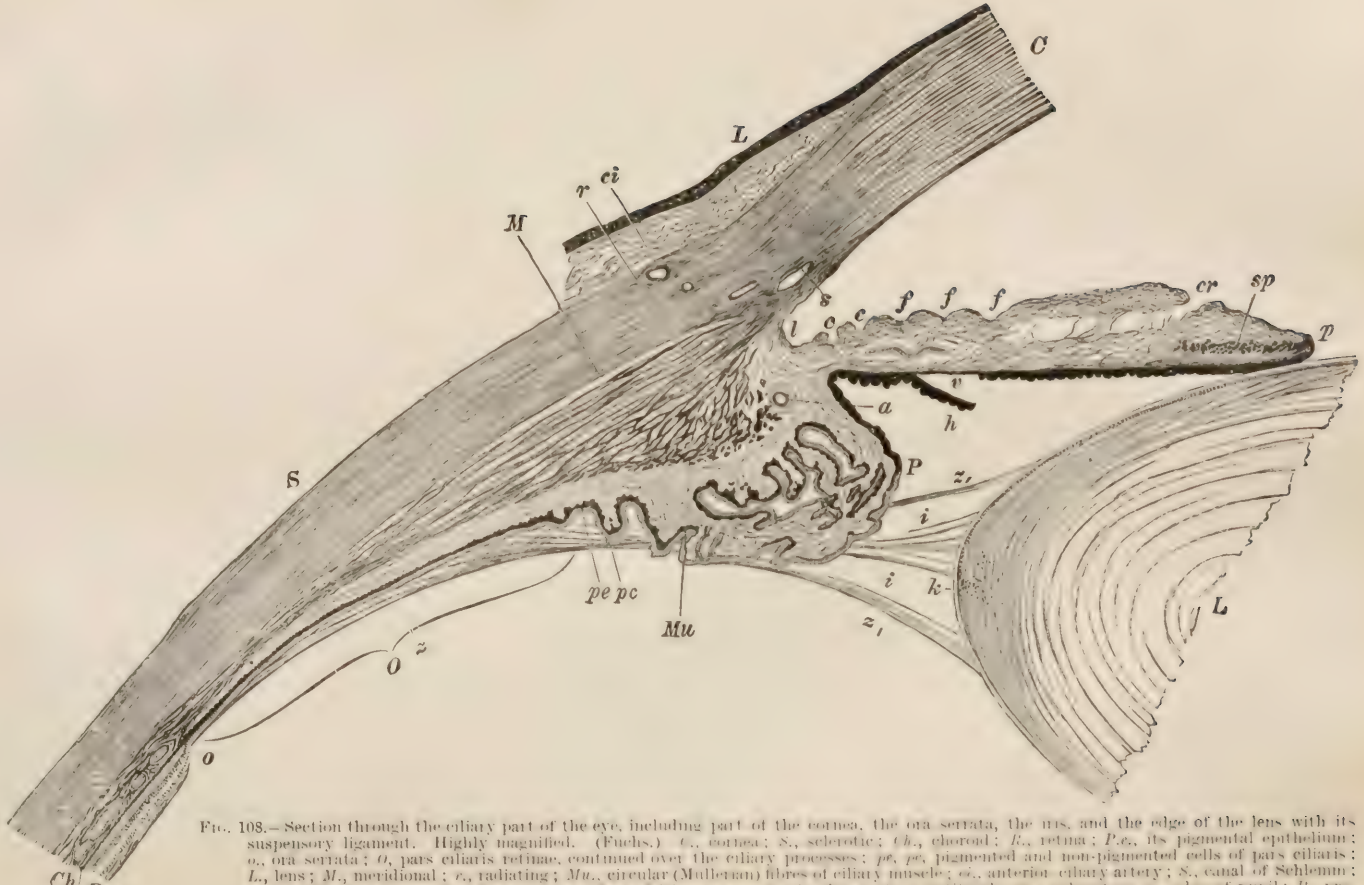


FIG. 108.—Section through the ciliary part of the eye, including part of the cornea, the ora serrata, the iris, and the edge of the lens with its suspensory ligament. Highly magnified. (Fuchs.) *C.*, cornea; *S.*, sclerotic; *Ch.*, choroid; *R.*, retina; *P.e.*, its pigmental epithelium; *o.*, ora serrata; *O*, pars ciliaris retinæ, continued over the ciliary processes; *pe*, *pc*, pigmented and non-pigmented cells of pars ciliaris; *L.*, lens; *M.*, meridional; *r.*, radiating; *Mu.*, circular (Mullerian) fibres of ciliary muscle; *ci.*, anterior ciliary artery; *S.*, canal of Schlemm; *c c*, *f f*, folds and depressions in anterior surface of iris; *cr.*, crevice in this surface (artificial); *sp.*, sphincter; *p.*, edge of pupil; *P.*, projecting part of ciliary process; *h*, pigment behind the iris (pars iridica retinæ) detached at *v*; *a*, blood-vessel; *z.*, zonule of Zinn; z_1, its continuation on the suspensory ligament; *i*, *i*, space between fibres of the suspensory ligament; *l*, capsule of lens.

ciliary margin of the iris is in relation with the base of Bruch's muscle and with the ciliary processes, and is continuous with the cornea by the ligamentum pectinatum. Between it and the cornea is the so-called iridic angle, which varies with the anterior curvature of the iris, and is of great importance to oculists. The colour of the anterior surface of the iris varies widely between turquoise blue, grey, yellow, and brown. The posterior surface is quite black owing to a layer of pigment epithelium, the continuation of that in the retina. The edge of the pupil lies close to the lens; the ciliary or posterior part forms the anterior wall of a triangular space filled with aqueous humour—the posterior chamber.

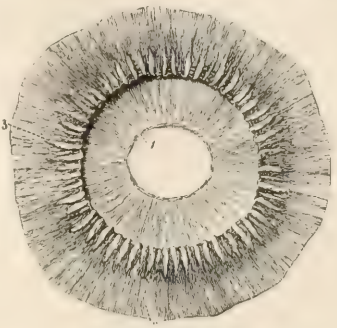


FIG. 109.—Ciliary processes seen from behind. Twice the natural size. 1, posterior surface of iris, with sphincter pupillae; 2, anterior part of choroid; 3, ciliary processes.

The tissue or stroma of the iris consists of cells and fibres of connective tissue, mostly arranged radially to the pupil. The specific colour which it reflects outwards is due to ramified pigmental cells resembling those of the choroid. Contiguous to the margin of the pupil there is a zone of smooth muscle-fibres circularly disposed, about 0·5 m. broad, known as the sphincter pupillae. There is also a layer of muscle-fibres, radially disposed and therefore acting antagonistically to the sphincter. They begin at the ciliary or outer edge of the iris, at the so-called membrane of Bruch, immediately in front of the pigment epithelium, and converge towards the pupil, where they bend round and lose themselves among those of the sphincter (Fig. 110). The existence of a true dilatator pupillae has been questioned by many authors, both in man and mammals. But it is now generally admitted that even if it does not consist of true muscle cells, like the sphincter, it is a continuous membrane, radially fibrillated, constituted of a specific myoid tissue.

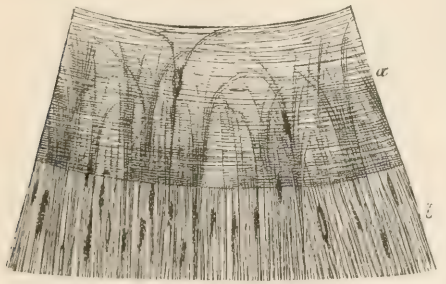


FIG. 110. Segment of the iris seen from posterior surface after removal of the uveal pigment. (Ivanoff.) *a*, sphincter muscle, of which only the deepest part is seen; *b*, dilatator muscle of pupil lying immediately in front of pigment cells.

The retina is a delicate membrane, of which the posterior part as far as the ora serrata contains the nerve-cells, from which the fibres of the optic nerve originate, as well as their end-organs.

The anterior or ciliary part consists only of a simple layer of a different constitution, destitute of nerve-fibres, which runs from the ora serrata to the apex of the ciliary processes, where it is limited to the black pigment layer, which is continued on to the posterior surface of the iris. The thickness of the retina diminishes from behind, forwards, from 0·5 mm. at the entrance of the optic nerve to 0·1 mm. near the ora serrata. We shall elsewhere discuss its different layers and more intricate structure.

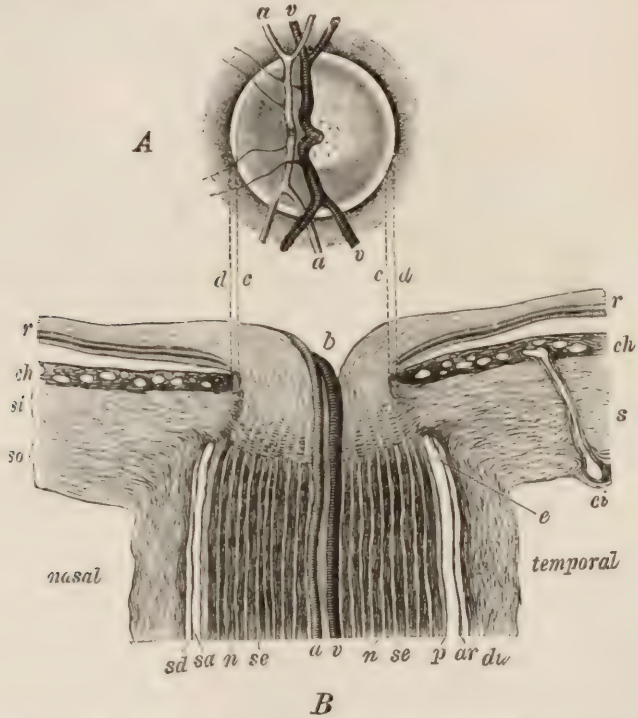


FIG. 111.—Section through the optic nerve at its entrance (*B*) and an ophthalmoscopic view of the disc (*A*) to show the corresponding parts. (Jaeger.) *c*, *d*, lines of correspondence; *b*, pit in centre of disc; *r.*, retina; *ch.*, choroid; *si*, *so*, inner and outer parts of sclera; *ci.*, a ciliary artery cut longitudinally; *a.*, *v.*, central artery and vein; *sd.*, sub-dural space; *sa.*, sub-arachnoid space; *dw.*, dural sheath; *ar.*, arachnoid sheath of nerve; *p.*, pial sheath; *n.*, nerve-bundles; *se.*, septa between them.

The optic nerve penetrates the eyeball, by perforating the sclerotic and choroid, and spreads out in the retina at a point which does not correspond with the posterior pole, but lies inside the geometric axis of the eye. Viewed superficially with the ophthalmoscope, the entrance of the optic nerve is seen as a disc known as the papilla nervi optici, its periphery is slightly elevated, but the centre, through which the retinal vessels emerge, forms a depression or pit (Fig. 111, *A*). In section, a number of

anatomical details are seen, as well as the relative thickness of the three principal coats of the eye and the optic nerve as it enters it (Fig. 111, *B*).

The interior of the eyeball contains the vitreous body, crystalline lens, and aqueous humour. The vitreous body takes up four-fifths of the eyeball. It is quite transparent, gelatinous in consistency, sub-globular in shape, with a depression in front to receive the lens and its capsule (fossa patellaris). At the periphery the whole vitreous body is covered with a delicate



FIG. 112.—Fibrous structure of adult lens. 1, anterior; 2, posterior; 3, lateral view. $\frac{2}{3}$. (Arnold.) In 3, *a.*, anterior; *p.*, posterior pole. The direction of the superficial fibres is indicated by the curved lines.

membrane, the hyaloid membrane. In the adult this has no vessels, and its nutrition is dependent on the surrounding vessels of the retina and ciliary processes.

The crystalline lens is an elastic transparent body of bi-convex form and rounded circumference, enclosed in an elastic membrane known as the capsule of the lens. Its anterior surface, which is in contact with the iris, represents a segment of a circle with a longer radius or curvature than that of the posterior surface, which rests upon the fossa patellaris of the vitreous body. The refractive power of the crystalline substance is greater than that of water, and increases from the periphery of the lens to its

central point. The body of the lens has a fibrous structure, and

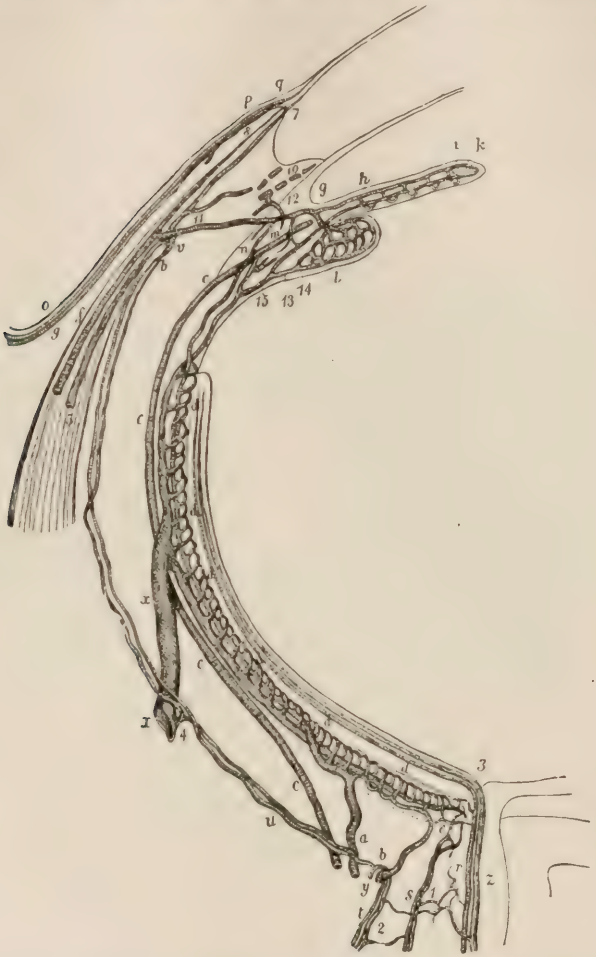


FIG. 113.—Diagrammatic representation of the course of the blood-vessels in the eye. (Leber.) *a* and *b*, short posterior ciliary arteries; *c*, long posterior ciliary arteries; *d*, *d*, *d*, capillary network or chorio-capillaris; *e*, arterial twigs that penetrate the optic nerve; *f*, anterior ciliary arteries; *g*, circulus vascularis iridis major; *h*, artery of iris; *i*, circulus vascularis iridis minor; *k*, capillary plexus in region of iris sphincter; *l*, artery of ciliary process; *m*, artery of ciliary muscle; *n*, recurrent artery of choroid; *o*, posterior artery, *p*, anterior artery of conjunctiva; *q*, arterial twig of pericorneal plexus; *r*, central artery of retina; *s*, artery of inner sheath, *t*, of outer sheath of optic nerve; *u*, sclerotic branch of short ciliary artery; *v*, sclerotic branch of anterior ciliary artery; *x*, one of the vorticose veins; *y*, posterior ciliary veins; *z*, central vein of retina; 1, vein of inner, 2, vein of outer sheath of optic nerve; 3, venous and arterial twigs of choroid, penetrating the optic nerve; 4, sclerotic vein, opening into a vorticose vein; 5, anterior ciliary vein; 6, its sclerotic branch; 7, veins of pericorneal plexus; 8, anterior, 9, posterior conjunctival veins; 10, ciliary plexus; 11, twig uniting it with the anterior ciliary vein; 12, veins of ciliary muscle, passing into ciliary plexus; 13, veins of ciliary process; 14, veins of iris; 15, veins of ciliary muscle, passing into a vorticose vein.

consists of fibres which are arranged in concentric layers and lie

in a regular stellate, radial direction (Fig. 112). A membrane is attached to both the anterior and the posterior surface of the capsule of the lens; these two membranes converge towards the ciliary processes and unite with them, forming the two layers of the so-called ligamentum suspensorium lentis, or zonule of Zinn. It is generally held that this ligament arises from the doubling of the hyaloid membrane. The anterior, more highly developed layer follows the inflexions and eminences of the ciliary processes, and forms the prolongation of the zonule of Zinn and the inner limit of the posterior chamber. The posterior layer is continued from the more flattened surface of the ciliary processes over the anterior surface of the vitreous body. The circular space, triangular in cross-section, enclosed between the two layers, is known as Petit's canal. The hyaloid membrane, being united to the uvea, follows the movements imparted to the latter by the ciliary muscle.

The space taken up by the aqueous humour is, as we have seen, divided by the iris into an anterior and a posterior chamber. The latter communicates by small slits in the anterior layer of the suspensory ligament of the lens with the canal of Petit. The aqueous humour is a clear fluid of lymphoid nature, which contains a few leucocytes. It is probably secreted by the epithelium of the ciliary body and its glandular crypts. It communicates by means of the slits in the ligamentum pectinatum iridis with the lymph spaces and the canal of Schlemm.

In order to understand the blood-supply of the eye we may profitably study Leber's diagram (Fig. 113). In it can be distinguished the short and long posterior ciliary arteries, which perforate the sclerotic near the entrance of the optic nerve; the anterior ciliary arteries, which perforate the sclera near the points of attachment of the outer muscles of the eye; and the large vorticose veins, which leave the sclera behind the equator of the eye. These vessels supply the different parts of the uvea as well as the sclera. The cornea is entirely destitute of blood-vessels. The course of the arteries and veins in the choroid, as shown by Fig. 114, is characteristic. The vascular supply of the retina is distinct from that of the uvea; it consists of the ramifications of the central artery and veins, which run along the axis of the optic nerve, as seen in Fig. 111. The two vascular systems communicate by means of anastomoses at the entrance of the optic nerve.

The outer and middle coats of the eye are supplied by countless nerves, which give them sensibility and innervate the ciliary muscles and muscles of the iris, as well as the muscle-fibres of the blood-vessels. These are the ciliary nerves, derived from the ciliary ganglion, which lies in the posterior part of the orbit (Fig. 115). The ciliary ganglion receives a sensory root

from the nasal branch of the ramus ophthalmicus of the trigeminus, a motor root from the oculo-motor, and afferent and

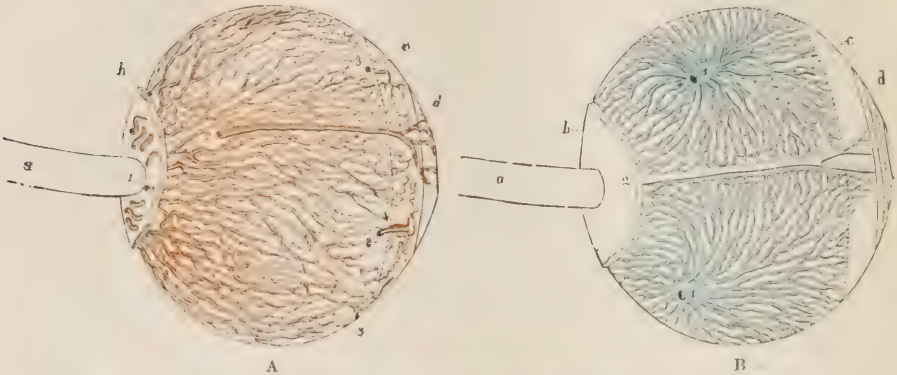


FIG. 114.—A, arteries of the choroid and iris, lateral view; B, veins of the choroid, lateral view. (From Arnold.) *a*, optic nerve; *b*, part of sclerotic left behind; *c*, region of ciliary muscle; *d*, iris; 1, posterior ciliary arteries piercing sclerotic and passing along choroid; 2, one of the long ciliary arteries; 3, anterior ciliary arteries; 1, 1, two trunks of the venae vorticosae at the place where they leave the choroid and pierce the sclera.

efferent roots from the plexus cavernosus of the sympathetic. The long and short ciliary nerves are given off from the ganglion and sympathetic plexus, and penetrate by the posterior part of the sclera in 12-20 little bundles to the eye, run across its posterior surface, and are ultimately distributed to the ciliary body, iris, and cornea (Fig. 116).

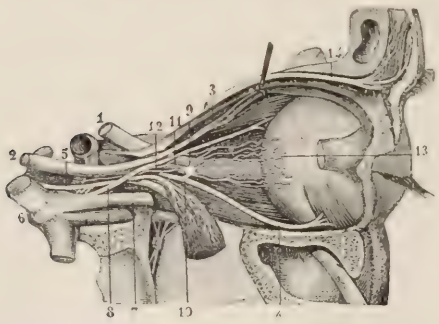


FIG. 115.—Nerves of the orbit, lateral view. Reduced $\frac{3}{4}$. (Sappey.) The ramus externus is divided and turned back. 1, optic nerve; 2, trunk of third nerve; 3, its superior division to the levator palpebrae and rectus superior; 4, its lower and longer branch to the inferior oblique; 5, sixth nerve joined by branches of the sympathetic; 6, Gasserian ganglion; 7, ophthalmic nerve; 8, its nasal branch; 9, ciliary ganglion; 10, its short, 11, long, 12, and sympathetic roots; 13, short ciliary nerves; 14, supra-orbital nerve.

II. From the physiological standpoint two parts must be distinguished in the structure of the eyeball: the retinal portion of the inner coat, containing the expanded termination of the optic nerve, on which the specific function of the eye as the peripheral organ of vision depends, and the other parts of the eye, which constitute a complicated dioptric system.

This physiological distinction is sanctioned by the embryological development of the eye (for which see Text-books of

Embryology and a recent Monograph by Cirincione). The vitreous body, the uvea (choroid, ciliary zone, iris), and the outer coat (sclerotic and cornea) are mesodermal in origin; the inner coat alone is ectodermal in origin, and of the parts which constitute it (retina, zonule, crystalline lens) only the inner layer of the retina had in the adult the character of a sensorial tissue, composed, as we shall see, of specific neural elements—the outer layer remains as a single stratum of pigmented epithelial cells, in close functional relation with the nerve-cells of the retina.

Giambattista della Porta (1589) first discovered the optical instrument known as the *camera obscura*, which he compared to the eye, noting the correspondence of its parts: the convergent lens

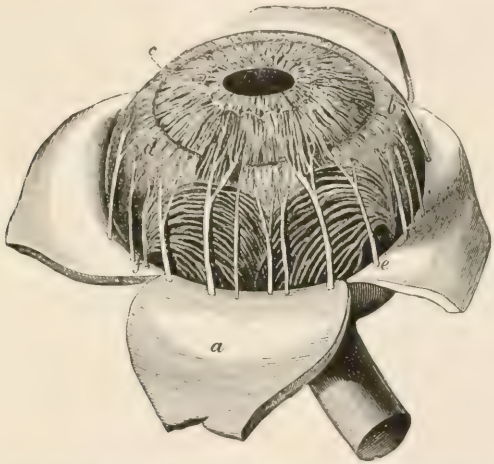


FIG. 116.—Choroid membrane and iris exposed by removal of the sclerotic and cornea. Twice the natural size. (Zinn.) *a*, part of the sclerotic turned back; *b*, ciliary muscle; *c*, iris; *e*, one of the ciliary nerves; *f*, one of the vasa vorticosa or choroidal veins.

of the camera obscura corresponds to the crystalline lens of the eye; the diaphragm corresponds to the iris, while the surface on which the reduced and inverted image of external objects is formed in the camera corresponds to the retinal surface of the eye. The dioptrics of the eye were first worked out systematically by Kepler (1602). But neither della Porta nor Kepler saw the formation of images on the retina. This was first demonstrated by Christoph Scheiner, a Jesuit Father, who observed it on the excised eye of freshly killed animals (1609), and also on the human eye when the retina was exposed at the back of the globe (1625).

The simplest method of seeing the formation of images at the back of the eye is that of Magendie (1836). He dissected the eye of an albino rabbit, and then, after removing all portions of the

tissue adherent to the sclerotic (which in albinos is fairly transparent), examined the posterior surface by turning the cornea towards a source of light, as a window, or in a dark room, towards a candle flame. But the retinal image is much plainer in the eye of large mammals like the ox, on cutting out posteriorly a piece of sclerotic and choroid of about the same size as the cornea. In the image thus formed on the retina external objects are greatly reduced, but all the outlines are clear and the colours are faithfully represented. The image is inverted, and every movement of the object is reproduced on the retinal image in the reverse direction. The size of the image decreases proportionately to the distance of the object.

To form a sharp image of the object, either on the sensitive plate of the photographic camera, or on the retinal surface of the eye, the light-rays starting from any point of the object must in passing through the corresponding dioptric system unite at given points of the receptor surface so as to form an inverted real image there. To understand this clearly, we must consider certain laws of optics:

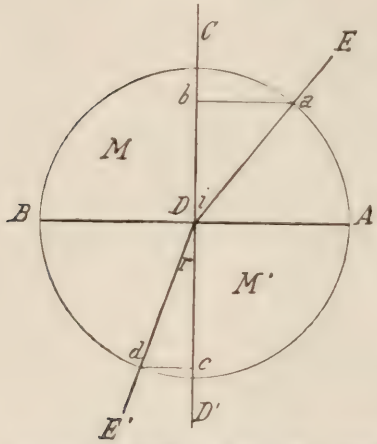


FIG. 117.—Refraction of a ray that passes through two media separated by a plane surface.

(*a*) *Index of Refraction.*—When a ray of light passes from one medium to another separated by a plane surface, it is refracted when it falls obliquely on the plane of separation of the two media. Let *MM'* be two media (Fig. 117), *AB* the surface of separation, *CD* a vertical, and *ED* an oblique ray. Then, as the diagram shows, *CD* goes from *M* to *M'* without deflection, while *ED* takes the direction *DE'*. The incident ray and the refracted ray are in the same plane. The angle *i* is called the angle of incidence, the angle *r* the angle of refraction. The relation between the sine of the angle of incidence and the sine of the angle of refraction or between *ab* and *cd* is called the refractive index. This relation is a constant, indicated by *n*, for two given media. In measuring *n* it is always assumed that the ray of light is passing from the air to a denser medium. On passing, for instance, from air to water the ray is so deflected that *ab* : *cd* is as 4 : 3. The refractive index of water is thus $\frac{4}{3}$, more exactly 1·336. That of glass is $\frac{3}{2} = 1{\cdot}5$. The sines of the angle of incidence and of refraction vary with the velocity of the pro-

pagation of light in the two media. If V and V' indicate the velocity in the two media, then $n = \frac{V}{V'}$.

(*b*) *Refraction of Light in a Simple Convergent System.*—The laws of refraction are the same when two refractive media are separated by a curved surface and by a plane surface. The difference in the effects obtained depends solely on the fact that the direction of the normal varies from one point to another when the surface is curved, while it is constant on a plane surface. Let MM' (Fig. 118) represent two differently refracting media, separated by the spherical surface AB, the centre of curvature of which lies at C in the plane of section; all radii of this circle drawn from C would fall perpendicularly in the corresponding tangents of the spherical surface, and are called *directive lines.* Directive lines which pass from M to M' in a plane perpendicular to the corresponding tangents, as PC, $P'C$, are not refracted, and meet at C,

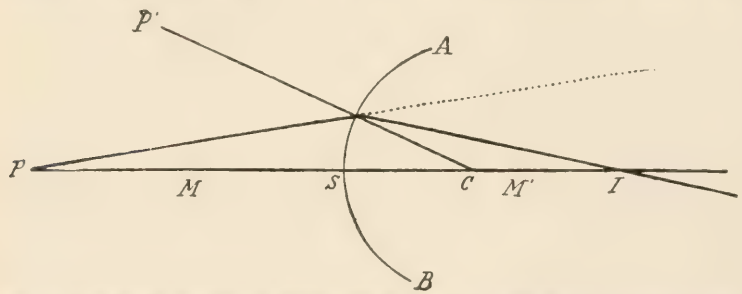


FIG. 118.—Refraction of a ray that passes through two media separated by a spherical surface.

which is, as we shall see, the nodal point of the convergent system. All other rays, on the contrary, which fall obliquely upon the surface AB from the point P, are refracted on reaching the medium M'. If we suppose that another ray from point P falls obliquely on the curve AB, it is refracted approximately into the direction of PC, so that at I it meets the line PC, which is called the principal axis or optical axis of the system. All other rays from the point P that fall on the spherical surface are more or less refracted according to their greater or less obliquity, so that they all converge towards I. This, however, is true only of the cone of rays that form an acute angle with the optical axis, *i.e.* the rays which fall on the refractive surface at an angle closely approximating to a right angle. For such rays point I coincides with the image of the object represented at point P.

If, on the contrary, the luminous point lies in M', the more highly refractive medium, the rays from I that fall on the concavity of the spherical surface converge after refraction at P, for by the law of reciprocity light-rays passing from M' to M take the

same path as those passing from M to M'. The two points P and I, that is, the object and the image, between which these reciprocal relations exist, are termed conjugate foci.

The distance of the conjugate focus I from the point S on the refractive surface through which the optical axis passes, depends on the distance of the luminous point P. When the distance PS increases, the distance SI decreases, and *vice versa*; in other words, the conjugate foci are displaced in the same direction.

(*c*) *Focal Points and Focal Planes.*—When rays of light passing from M to M', or from M' to M, and separated by a spherical surface, come from a point at infinite distance lying on the principal axis, *i.e.* when they are parallel to each other and to the principal optical axis, they converge after refraction at a point on the axis known as the *principal focus*. This again is distinguished as anterior or posterior, according as the parallel rays pass from M to M', or from M' to M.

In Fig. 119 the parallel rays represented by RA, RB pass from

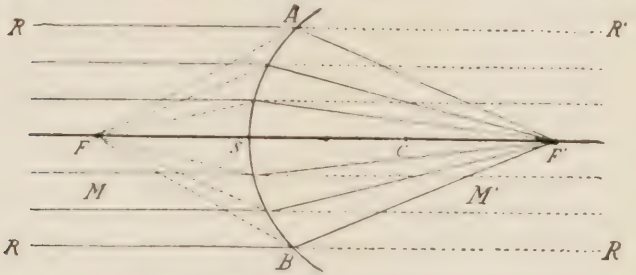


FIG. 119.—Diagram to show the principal focal points and focal planes.

M to M', and the posterior focal point lies at F'; the parallel rays passing from M' to M are represented by the dotted lines $R'A$ and $R'B$, and the anterior focal point lies at F. The distances between the two foci $F'F$ and the refracting surface S are the focal distances, FS the anterior, $F'S$ the posterior focal distance. The planes perpendicular to the optic axes, which pass through the foci, are the anterior and posterior focal planes.

(*d*) *Construction of an Image from a given Object.*—Let M be the first and M' the second medium (Fig. 120), AB the spherical surface of separation, C its centre of curvature, FF' the anterior and posterior focal points on the optical axis of the system, and O the object. To determine the image of O in M', draw the directive line OC which is not refracted, and then the line OH parallel to the optical axis, which passes after refraction through the posterior focal point F'; point I at which the two rays intersect coincides with the image of O. So, too, the image I' corresponds in M' to the object O' in M, and the whole object OO' corresponds to the real inverted image II'. It is obvious from the geometrical con-

struction of the figure that the size of object OO' is to the size of image II' as the distance of the object from the nodal point C is to the distance of the image from the same point.

(*e*) *Refraction of Light in a Centred Optic System.*—A more complex dioptric system, as that of the eye, results when several spherical surfaces are separated by media with different refractive indices. When the centre of curvature of the respective surfaces of separation are all on the same straight line, given by the optic

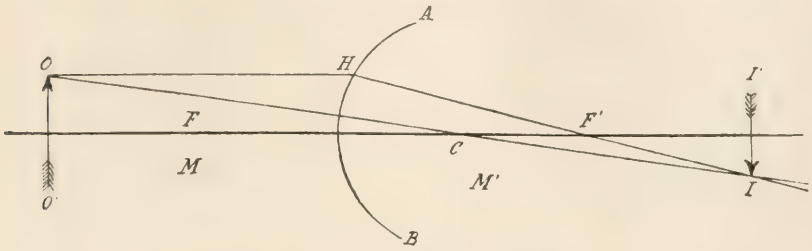


FIG. 120.—Formation of the image of a point.

axis of the system, the system is said to be *centred*. In order to determine the refraction of such a complex system, *i.e.* to construct the image of a given object, it is necessary to pass from medium to medium according to the above rules. Gauss (1841), by mathematical calculation, demonstrated that the determination of refractive power in any compound, centred system can be greatly simplified if the radii of curvature of the respective surfaces of

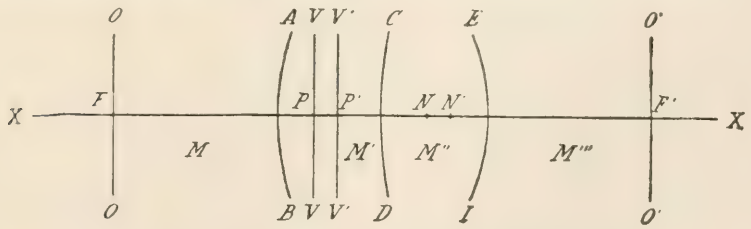


FIG. 121.—The six cardinal points of a centred dioptric system.

separation, the refractive indices of the different media, and their relative position upon the optical axis of the system are known. He showed that each centred system may be replaced by a system of six cardinal points (optic constants of Gauss). Given, for instance, a system of four refractive media (M, M', M'', M'''—Fig. 121) separated by the three spherical surfaces AB, CD, EI, which all have their centre of curvature on the straight line XX formed by the optic axis, the fundamental law laid down for a simple system still holds good—viz. that a definite point on the image corresponds to each point of a luminous object.

Of the six cardinal points the first two are represented by the foci FF'. The posterior focus F' is, as we have seen, that at which all parallel rays entering the system converge after refraction; the anterior focus F is that at which all parallel rays converge on leaving the system. The planes OO, $O'O'$, which cut the foci vertical to the optical axis, are the focal planes of the system.

Between the two foci lie the two principal points PP'. Through these the two principal planes VV and $V'V'$ pass vertical to the axis.

Each incident ray that passes through P leaves by P'; each ray that passes through any point of the plane VV passes through a corresponding point, equidistant from the axis, of the plane $V'V'$. In other words, P' is the optical image of P, and the several points of the plane $V'V'$ are the erect optical image, equal in size, of the corresponding points of the plane VV. The distance FP is called the *anterior focal*, $F'P'$ the *posterior focal*

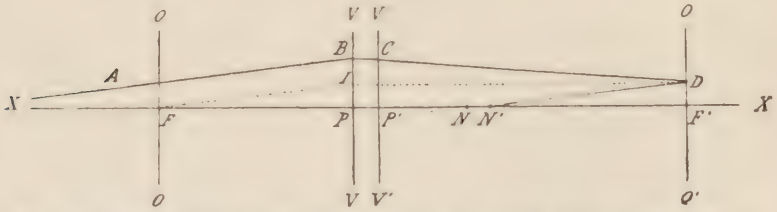


FIG. 122.—Refraction of an incident ray passing through a centred system, constructed from the six cardinal points.

distance. The position of the two principal points must be calculated.

Between P' and F' are the two nodal points, NN', the optical centres for the two surfaces VV, $V'V'$. The distance between the two principal points is equal to that of the two nodal points; hence the distance FP is equal to the distance $F'N'$. The nodal points are characterised by the fact that a ray which passes from the first medium to the first nodal point N also passes through the second nodal point N', the refracted and the incident rays being parallel.

(*f*) *Course of a Refracted Ray in a Centred System.*—When a system with differently refracting media is replaced by the six cardinal points, it is easy to make a diagram of the path of any refracted ray.

Let AB be an incident ray (Fig. 122); from point B draw a parallel to axis XX, which cuts the second principal plane $V'V'$ at the point C; then draw from the second nodal point, parallel to the incident ray AB, a line $N'D$, which cuts the posterior focal plane $O'O'$ at D; on joining C and D, the line CD gives the direction of the refracted ray. The same result is obtained if the

straight line FI is drawn from the anterior focus F parallel to the incident ray AB, and the straight line ID from point I parallel to the axis XX'; on joining point D, where the line cuts the posterior focal plane $O'O'$, with C, the line CD gives the direction of the refracted ray.

(*g*) *Construction of the Image of a given Object in a Centred System.*—To determine the position on the image of point A of the luminous object AB (Fig. 123), it is only necessary to know the path of two rays starting from this point. If a first line AC is drawn parallel to the axis, which cuts the second principal plane $V'V'$ at C, it must—in consequence of refraction—pass through the posterior focal point F', in the direction of $CF'A'$. On drawing a second line from A in the direction of the first nodal point N, and a parallel to AN from the second nodal point N', this cuts the line $CF'A'$ at A', the image of the object A. By the same process the image of the object B coincides with B'. The whole

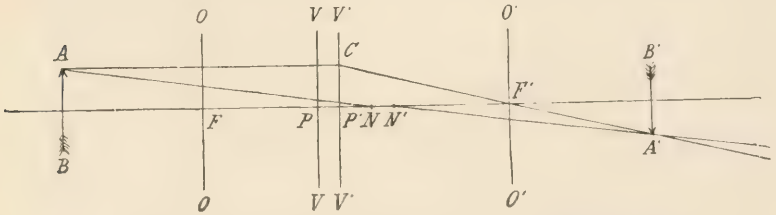


FIG. 123.—Formation of the image of a point in a centred system.

image $A'B'$ of the object AB is an inverted real image, as can be seen upon a projected plane.

(*h*) *Refraction of Light through Convex and Concave Lenses.*—Lenses may be taken to represent a compound dioptric system, in which the extreme media have the same refractive index, which is lower than that of the central medium, and in which the two refractive surfaces are at a less distance from each other than the respective centres of curvature.

In lenses the principal points coincide with the nodal points. The optical centre of the lens is taken as that point of the optic axis at which a ray of light is not deflected. The distance of the optical centre from the two refractive surfaces of the lens is in proportion to the radii of the surfaces.

The refractive power of a lens is greater in proportion as its focal distance is less, *i.e.* is inversely proportional to the focal distance. A lens with a focal distance of 1 m. is usually taken as the unit strength, and the refractive power of such a lens is called a diopter (D.). Lenses of 2, 3, 4 . . . D. have, respectively, focal distances of $\frac{1}{2}$, $\frac{1}{3}$, $\frac{1}{4}$. . . of a metre.

Convex are distinguished from concave lenses. The former have a *positive* focal distance. They cause the parallel rays

passing through them to converge at the focal point, or *vice versa* cause the divergent rays from the focal point to become parallel. The rays from an object on the optical axis beyond the focal point converge on the other side of the lens in an image (Fig. 124). The farther or nearer the object from the focal point, the nearer or farther will be the image on the other side of the lens. If the light-rays proceed from any point on the optical axis between the focal point and the optic centre of the lens, then after passing through the lens they become less divergent, but are

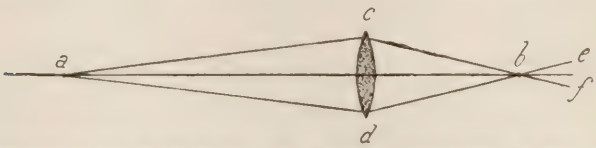


FIG. 124.—Convergent action of a bi-convex lens. *a*, origin of divergent rays, *ae*, *ad*, which beyond the lens become convergent, *cf*, *db*, and cross at *b*, which is the image of point *a*.

still unable to form an image. Finally, if a ray of light passes through a secondary axis, oblique to the lens, the same laws obtain, so long as it only forms a moderate angle with the optical axis.

Concave lenses have a *negative* focal distance (Fig. 125). They make parallel rays divergent, divergent rays still more divergent, and convergent rays less convergent or divergent.

Lenses with convex-concave or concave-convex surfaces are

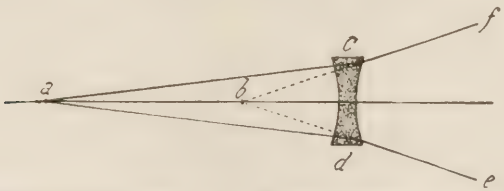


FIG. 125.—Divergent action of a bi-concave lens. *a*, origin of divergent rays, *ae*, *ad*, which beyond the lens become more divergent, *cf*, *de*, as if they came from point *b*, not from point *a*.

convergent or divergent according as the convex or concave surface has the shorter radius of curvature.

III. The dioptric apparatus of the eye consists in a highly complex system of refractive media, separated by spherical centred surfaces. From the front backward these are the cornea, moistened by a very thin layer of lachrymal secretion, the aqueous humour, the many variously refracting layers of the lens, and the vitreous body (humour).

To determine the path of the light-rays which traverse the eye to the retinal surface it is necessary to ascertain (*a*) the refractive indices of the different transparent media; (*b*) the radii

of curvature of the limiting surfaces; (*c*) the distance of these from each other and from the surface of the retina.

(*a*) The facts collected by various authors in relation to the refractive indices of the different transparent media of the eye, extracted from the living body or fresh cadaver, differ very slightly. The following table shows the figures obtained with the most reliable methods, particularly with Abbé's refractometer :—

Refracting Medium.	Index of Refraction.	Author.
Cornea	1·3771	Matthiessen.
Aqueous humour	1·3374	Hirschberg.
Capsule of lens	1·3599	Matthiessen.
Outer coat of lens	1·3880	
Middle coat of lens	1·4060	
Nucleus of lens	1·4107	
Vitreous body	1·3360	Hirschberg.

Comparison of these figures brings out two important facts: the refractive indices of the aqueous humour and the vitreous humour are approximately the same; the crystalline lens is not an optically homogeneous body, but consists of concentric layers of different consistency, so that the refractive index increases progressively from the periphery to the more central layers. To facilitate the study of dioptrics in the eye we may picture the crystalline lens as replaced by an optically homogeneous lens of the same form and the same total power of refraction as the lens. This can be determined directly on lenses extracted from the dead body and suspended in the air, to ascertain the position of the focal points; or it may be calculated from known data of the refractive indices of the different strata of the lens.

By both methods Matthiessen arrived at the result that the *total index* of the crystalline lens is 1·4371, which is considerably above the refractive index of the nucleus of the lens. According to Tscherning the total index given by Matthiessen is too high—he thinks 1·42 nearer the true figure. More recently (1902) Treutler has deduced the total refractive index of the lens from the diminution of refracting power in the eye that has lost its lens, and estimates it at 1·4215, which almost exactly coincides with that of Tscherning.

Neglecting these slight differences, it is remarkable that the total index of the lens is higher not only than the mean index of its different layers, but also than the maximal index of its nucleus. This fact, which at first seems paradoxical, is easily understood if we reflect that the nucleus of the lens is limited by far more highly convex surfaces than the lens as a whole, and the latter accordingly has a higher refractive index than a homogeneous lens con-

sisting of a medium of the same refractive index as the nucleus of the lens. According to Hermann we may conceive the lens to be formed of a highly bi-convex lens *a* and two concave-convex lenses *a* and *b* (Fig. 126). "The latter neutralise part of the effect of *c*, and the less so in proportion as their refractive index is lower. Since *a*, *b* have a lower refractive index than *c* the total action of the lens is greater than if it had the same index as *c*, *i.e.* if the lens were homogeneous and had the high refractive power of the nucleus throughout."

It will be seen later on that the stratified constitution of the lens is not without importance in the dioptrics of the eye.

We stated that the refractive index of the cornea is rather higher than that of the lachrymal secretion and the aqueous humour, which bathe its two surfaces. But from the point of view of optics the study of the eye is considerably simplified by the fact that the cornea is a lamella with parallel surfaces, and is therefore, like a watch glass, unable to alter the direction of a ray of light passing through it, and is capable only of slightly displacing it parallel to itself. The cornea may therefore be neglected and the eye considered diagrammatically as though it consisted of three media only, the aqueous humour, lens and vitreous body separated by surfaces that are approximately centred.



FIG. 126.—Diagram to show the physical structure of the crystalline lens, which consists of a strongly bi-convex central lens *c*, and two peripheral concave-convex lenses *a* and *b*. (After Hermann.)

(*b*) Petit (1723) attempted to estimate the radius of curvature of the cornea and the two surfaces of the lens, on eyes extracted from the dead body. These measurements, however, were very incomplete and unreliable, owing to the rapid shrivelling of the tissues, and Kohlrausch's method was afterwards adopted, in which the height of the images reflected from the corneal surface and the anterior and posterior surfaces of the lens are measured in the living eye. These are known as the Sanson-Purkinje images, from the authors who first described them.

The radius of curvature of the cornea is estimated by measuring the height of the corneal image of a luminous object, the size and distance of which are known, starting from the law that the size of the luminous object is to that of its reflected image as the distance of the luminous object from the convex surface of the mirror is to the half of the mirror's radius. Two points of light are generally employed as the luminous object. The distance of the images from the two points is measured by the ophthalmometer (of Helmholtz, Aubert, or Javal).

To observe Purkinje's images the flame of a candle must be placed about 50 cm. away at the height of the observer's eye, so that the line which unites the flame with the observed eye forms

an angle of about 35 degrees with the optic axis of the latter. The subject is asked to look fixedly at a distant point, in order to exclude all play of accommodation (*infra*). The observer brings his eye at the distance required for clear vision to the same level as the eye observed, so that his optic axis forms much the same angle as that formed on the other side by the rays of the flame, with the observed eye. Under these conditions the observer easily sees three different images of the flame in the pupil of the observed eye, in the order indicated by Fig. 127, when the flame is at the left.

The image *a* of medium size is the clearest, with sharp outlines; it is an erect, virtual image, reflected from a convex mirror, represented by the surface of the cornea. The image *b* is also erect, because it is reflected from a convex surface, namely the anterior surface of the lens; it is less bright, with less distinct outlines, because only a few rays are reflected, since there is little difference in the refractive indices of the aqueous humour and the lens; it is much larger than that reflected from the cornea, because it comes from a less convex mirror. If the observer moves his eye slightly to one side the image *b* is displaced considerably in the same direction. This means that the formation of this image is behind the pupil.



FIG. 127.—Images of a candle-flame, reflected from the cornea *a*, anterior surface *b*, and posterior surface *c* of the lens.

The third image *c* is inverted, and is thus a real image, reflected from a concave mirror, formed by the back of the lens. It is much less clear, because the number of rays reflected is less: it is smaller than the corneal image, because it is reflected from a mirror with a smaller radius of curvature. When the observer's eye moves sideways, its position in the field alters very little, showing that the seat of its formation lies but little behind the plane of the pupil.

It is by no means easy to take ophthalmometric measurements of the mirror-surfaces in the living eye. In calculating the radius of curvature on the basis of the size of the images, the refraction of the rays reflected from the mirror surfaces must be taken into account. We need not discuss the devices employed to overcome this difficulty by means of special ophthalmometers. It is enough to cite the following values found by different authors:—

Radius of curvature of corneal surface . . .	6·852–8·151	mm.
„ „ „ anterior surface of lens .	2·900–4·09	„
„ „ „ posterior surface of lens .	5·13 –8·49	„

(*c*) The exact determination of the positions of the surfaces of separation between the different refracting media of the eye, *i.e.*

the distance of these from each other and from the retinal surface, also presents many difficulties in the living eye, since the measurements on longitudinal sections through the hardened eyeball of the cadaver do not correspond with the true proportions. Here we can only give in the form of a table the extremes cited by the most competent observers :—

Thickness of cornea in its central portion . .	0·45 1·37 mm.
Depth of anterior chamber	2·90 4·09 „
Thickness of lens	3·03 4·43 „
Distance of back of lens from retina . . .	15·00 mm. (average).

According to the mathematical theory of Gauss (1841) any

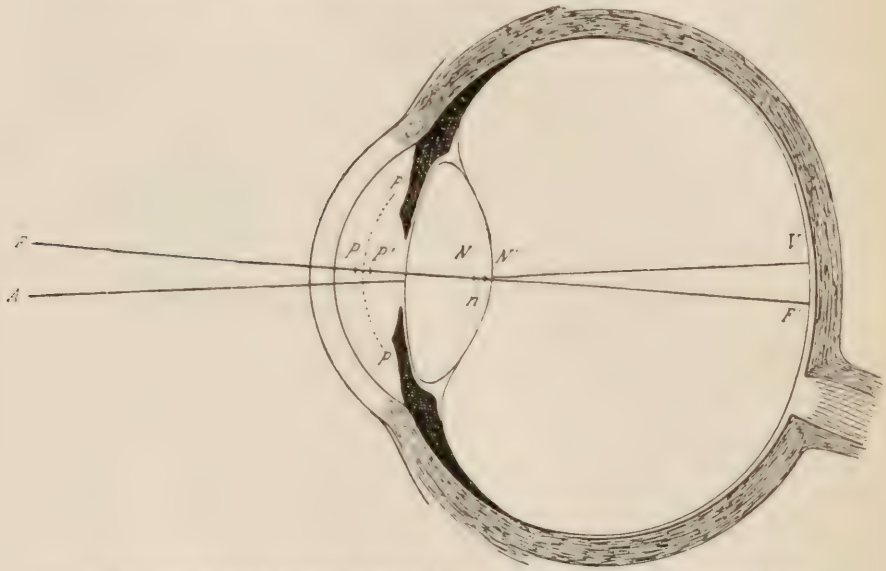


FIG. 128.—Position of the six cardinal points in Helmholtz' schematic eye. (Explanation in text.)

kind of centred dioptric system, no matter how complicated, may be replaced by a system of six cardinal points, as stated above. Moser (1844) first applied this theory to the eye, to determine the position of the two nodal points. Although the available data for the optic constants of the eye were still very imperfect, Listing (1847) not only completed the theory but ingeniously constructed a "schematic eye," which differed but little from that constructed by Helmholtz a few years later from the average of measurements made upon the living eye.

Helmholtz' schematic eye (Fig. 128) was constructed from the following averages of the optic constants of the eye :—

Index of refraction of the air	= 1·00
Index of aqueous humour and vitreous body	= 1·33

Index of lens as a whole	= 1·43
Radius of curvature of cornea	= 7·82 mm.
Radius of anterior surface of lens	= 10·00 „
Radius of posterior surface of lens	= 6·00 „
Distance of anterior surface of lens from cornea	= 3·6 „
Distance of posterior surface of lens from cornea	= 7·2 „

From these figures, and by applying the rules and calculations of Gauss to determine the position of the cardinal points on the axis of the total dioptric system of the eye, Helmholtz arrived at the results set out in the following table, in which the figures show the distance in millimetres of the cardinal points from the apex of the cornea:—

First principal point	(P)	1·75 mm.
Second principal point	(P')	2·1 „
Anterior focal distance	(F)	15·5 „
Posterior focal distance	(F')	20·7 „
First focal point	(P)	13·75 „
Second focal point	(P')	22·79 „
First nodal point	(N)	6·96 „
Second nodal point	(N')	7·32 „

Diagrammatically considered, therefore, the eye represents a convergent or collecting system with unequal anterior and posterior focal distances. The refractive index of the eye, measured from the posterior focal distance, amounts to 64·6 D.

As shown by Fig. 128, magnified three times from Helmholtz' figures, the two principal points (P, P') and the two nodal points (N, N') are so close together that there is practically no great error in taking the intermediate point p as the only principal point, and the intermediate point n as the only nodal point in the entire system. By this we arrive at the so-called "reduced eye," which consists of a simple convergent system, limited by a spherical surface p with a radius of curvature of 5 mm., which divides the air (refractive index = 1) from the vitreous body (refractive index = 1·33). The nodal point of this simple system lies close to the posterior surface of the lens. The refractive power of this reduced eye would be 66·67 D., which differs little from the average normal eye.

By means of this diagram it is easy to follow the course of the luminous rays that enter the eye, and to understand the formation of real images of external objects upon the retina. When the inverted image of a flame is formed, it must be assumed that each luminous point of the flame sends a bundle of divergent rays through the pupil, which, in consequence of refraction, converge at a corresponding point on the plane of the retina.

Fig. 129 indicates the course of the rays abc, $a'b'c'$ from the extreme ends of the object. The lines XX and YY from these two points, which cross at the nodal point n of the reduced eye and are projected, unrefracted, on to the retina after crossing, are

called *directive lines*. The angle formed by the two directive lines is the *visual angle*. From the visual angle formed by the two directive lines from the two extreme points of an object it is possible to calculate the size of the image projected on to the retinal plane of the dioptric system of the eye.

IV. In the normal resting eye the posterior focal point of the dioptric system coincides with the most external layer of the retina, in which are the peripheral nerve-cells that are sensitive to light. This is indispensable to the formation of a distinct image.

Emmetropia is the name given to that state of refraction of the resting eye in which the image of an object at infinite distance, the rays from which enter parallel to the eye, is projected directly upon the sensitive layer of the retina.

Emmetropic refraction is compatible with a varying refractive power of the dioptric system; it is only essential that there shall be a correct relation between the refractive power and the optical

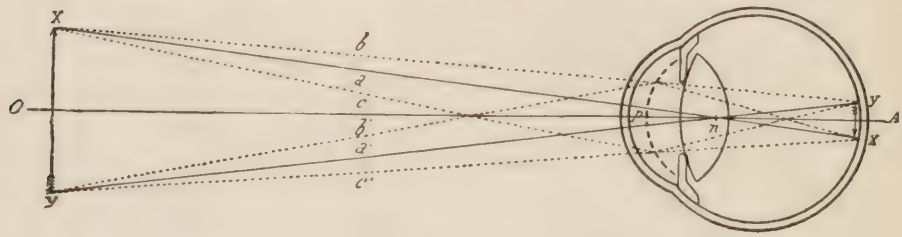


FIG. 129.—Formation of inverted image of an object on the retina of a reduced eye.

axis of the eye—that is, the distance of the principal point of the reduced eye from the sensory layer of the retina. Thus, *e.g.*, the reduced eye is emmetropic with the following combinations:—

Refractive power = 60 D.	Length of axis = 22·17 mm.
„ „ = 63 „	„ „ = 21·11 „
„ „ = 66 „	„ „ = 20·15 „

Ametropia is the state in which there is an incorrect relation between the refractive power and the length of axis of the eye at rest. It may result from abnormal values of the optic constants, or from abnormal length of the axis. Accordingly ametropia of the axes, of the radii of curvature, and of the refractive indices can be distinguished. By far the most frequent forms of ametropia are those due to excessive or defective length of the axes. The former constitute *myopia* or *hypometropia*, the latter *hypermetropia*.

In *myopia* (short sight), parallel rays, that is those coming from an infinite distance, are brought to a focus, not on the sensitive layer of the retina, but in front of it. In hypermetropia (long sight), on the contrary, they come to a focus behind it.

When his eye is at rest the myope cannot see distant objects distinctly, and the hypermetrope cannot see near objects distinctly, because in these opposite forms of ametropia diffusion-circles instead of images are formed on the plane of the sensitive retina, corresponding to the respective points of the object. *Diffusion-circles* are circular surfaces of illumination, which result from the transverse section of the cones of rays that enter by the pupil; when reciprocally superposed, these make the retinal image confused and indistinct.

This is clear from the diagram (Fig. 130), in which the states

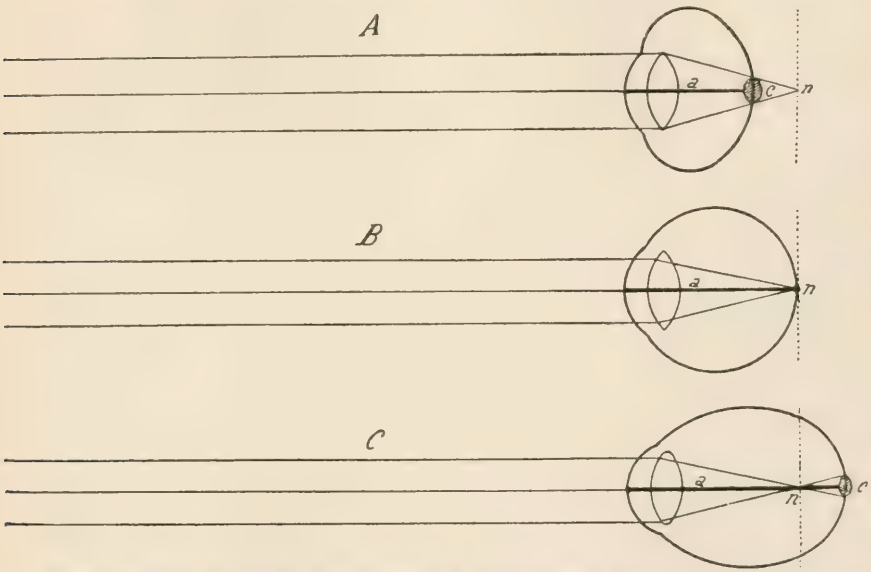


FIG. 130.—Diagram to show the static refraction of the eye. (After Cohn.) *A*, hypermetropic; *B*, emmetropic; *C*, myopic eye; *a.*, optic axis; *n.*, nodal point at which the parallel rays that enter the eye converge; *c.*, diffusion-circles.

of refraction of three types of eyes, resulting from different lengths of the axis, are compared.

The *far point* of the eye is that which forms a sharp image upon the sensitive layer of the retina when the eye is at rest. In the emmetropic eye it is at infinite distance; in the myopic eye objects at a definite distance are focussed in front of the retina; in the hypermetropic eye at a short distance behind. Accordingly, in myopia the relative refractive power of the eye is in excess, in hypermetropia it is too low.

The degree of myopia or of hypermetropia is determined accurately by the refractive power of the lenses (concave or convex) required to make the myopic or hypermetropic eye emmetropic in rest.

The following table shows the different degrees of ametropia that correspond to different lengths of the axis of the reduced eye:—

Length of Axis.	Degree of Ametropia.	Length of Axis.	Degree of Ametropia.
17 mm.	+11·8 D.	21 mm.	−3·2 D.
18 ,,	+ 7·5 ,,	22 ,,	−6·1 ,,
19 ,,	+ 3·5 ,,	23 ,,	−8·7 ,,
20 ,,	0 ,,	...	...

The refractive power of the eye at rest, that is its static refraction, alters with age.

The eye of the new-born, according to Horstmann, is in 88 out of 100 cases hypermetropic. The curvature of the cornea in the new-born is rather greater than in the adult; the lens is almost round, the anterior chamber much flattened, and the degree of hypermetropia varies between 1 and 6 D. During infancy and adolescence, up to the tenth year, the hypermetropia diminishes slowly, until the sight becomes emmetropic; but in the majority of cases a slight degree of hypermetropia persists throughout life, particularly in individuals who do not go to school. The investigations of Falkenberg and Straub on recruits showed that young people who appear to have normal sight are in many cases slightly hypermetropic when the eye is under the influence of atropine, which paralyses the activity of the ciliary muscle.

Myopia is very rare in infancy; but the percentage increases with age, particularly among school children.

In later years, at about fifty, emmetropic eyes become slightly hypermetropic, and eyes that are somewhat hypermetropic become more so, apart from the weakening of the mechanism of accommodation due to age. This fact depends on the changes brought about by age in the structure and composition of the lens.

In the different forms of ametropia the sight, owing to diffusion-circles, is confused and indistinct in direct proportion to:—

(*a*) The degree of ametropia, that is, as the retina is farther removed from the plane on which the image is formed.

(*b*) The size of the cone of rays which penetrate the pupillary aperture, that is, to the size of the pupil which limits the cone.

In both these cases there is increased width of the diffusion-circles, which produces a confusion of points and consequent indistinctness of the outline of the images. If we look through a small hole made by a pin in a card (stenopaic diaphragm) the luminous cone that enters the eye is small, and the images become sharper in proportion as the diameter of the diffusion-circles is reduced. This is plain from Fig. 131, in which *ab* represents the outline of a wide, *cd* of a narrow pupil; *O* is the object, *I* the

image; *rr* is the emmetropic position of the retina; *r'r'* the hypermetropic position; *r'' r''* the myopic position, relatively to the position of the two focal points *O* and *I*. With the wide pupil *ab* there are wide diffusion-circles *a'b'* and *a''b''*; with the narrow pupil *cd* the circles are less in diameter, *c'd'*, *c''d''*.

V. We have seen that the emmetropic eye at rest has its posterior focal point in the sensitive outer layer of the retina, and is therefore able to see very distant objects. But in order to see distinctly near objects which are projected in a plane behind the retina the emmetrope must be able to increase the refraction of his eye by a proportional increase in the curvature of the lens. This active increase of the refractive power of the lens so as to adapt it to the distinct vision of near objects is the special function of the muscular mechanism that is associated with the dioptric apparatus of the eye—and is known as *accommodation*. To distinguish between the clear emmetropic vision of distant objects in repose without active intervention of the mechanism of

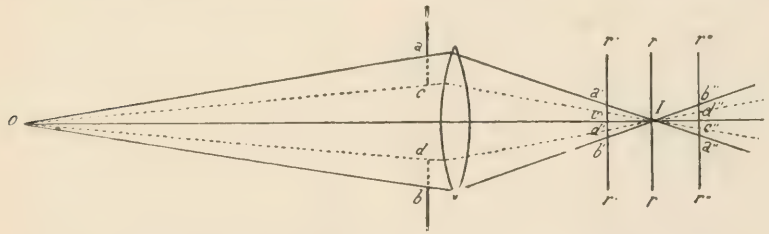


FIG. 131.—Diagram to show how the diffusion-circles alter when the pupil is contracted.

accommodation and the distinct vision of near objects in which such active intervention is required, the former is termed *vision by static refraction*, the latter *vision by dynamic refraction*.

The degree of adaptation, *i.e.* of active increase in the curvature of the lens, rises gradually with the nearness of the fixed object to the eye. The following table gives the position of the image with different distances of the object, calculated for the reduced eye:—

Distance of Object.	Position of Image.	Distance of Object.	Position of Image.
∞	20·00 mm.	0·50 m.	20·62 mm.
5 m.	20·06 ,,	0·25 ,,	21·27 ,,
1 ,,	20·30 ,,	0·125 ,,	23·57 ,,

Accordingly when the object is at a distance of 5 m. from the reduced eye the image is only moved back 0·06 mm.

As the sensitive layer of the retina is just about that thickness (0·06 mm.) it follows that at a distance of 5 m. the emmetropic

eye is not obliged to use its mechanism of accommodation in order to see objects distinctly. But if the object comes nearer than this the plane on which the image is formed is too far away from the sensitive layer of the retina; accordingly vision by simple static refraction is indistinct, and it is necessary to bring dynamic refraction into play in order to see distinctly.

It was long held that accommodation in the eye took place as in the photographic camera, which is adapted to different distances by shifting the sensitive plate to a greater or less distance from the lens. That is, the retina was thought capable of forward and backward movement, by means of the external oculo-motor muscles. But it was subsequently recognised that another, more perfect mechanism controlled the accommodation of the eye.

Descartes (1636) first suggested that distinct vision of objects at different distances depends on the power of the eye to alter the form of the lens. But the objective proof of this theory was only discovered two centuries later by M. Langenbeck, Cramer, and Helmholtz (1849–53).

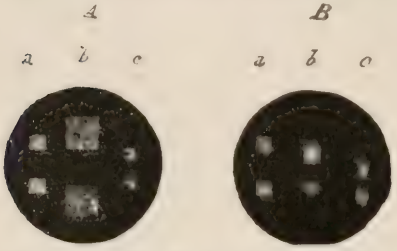


FIG. 132.—To show the alterations in Purkinje's images when the eye passes from static to dynamic refraction, in accommodation. (After Helmholtz.) *a*, image reflected from the cornea; *b*, from the anterior; *c*, from the posterior surface of the lens; *A*, during distant vision; *B*, during near vision.

As we saw (Sanson-Purkinje images, p. 286), the length of the radii of curvature of mirror-images reflected from the spherical surfaces of the cornea and lens can be calculated fairly accurately from the size of the image. If, while observing these images, the subject is told to focus a near object it will be seen that the image reflected from the cornea does not alter, while the image from the front of the lens, on the contrary, becomes much smaller, showing that the convexity of the mirror increases during accommodation. The image reflected from the back of the lens also becomes smaller, but in so slight a degree as to be unimportant. The experiment is easier if the image of two luminous squares is reflected from the eye instead of the image of a candle flame. It is then seen (Fig. 132) that the two images from the front of the lens are not only reduced, but are brought together, on accommodation.

Knapp (1860) determined on four eyes the position of the near and the far points, and the curvature and position of the cornea and surfaces of the lens in distant vision and during accommodation for near vision, and found that the alteration in the curvature of the lens suffices to explain the increased refractive power of the eye in focussing a near object.

During the change in form of the lens its posterior surface

remains practically unaltered, while the anterior surface, on the contrary, bulges with the increase in curvature, and also pushes the central margin of the iris forward and constricts the aperture of the pupil. This is obvious on watching the eye of any one who looks alternately at far and near objects. In distant vision the aperture of the pupil is seen as a long black line; in near vision the margin of the iris moves forward, and the pupil is narrowed (Fig. 133). According to Helmholtz the displacement of the anterior capsule of the lens in accommodation varies between 0·36 and 0·44 mm.

Another very important factor in accommodation is the lateral displacement of the lens, which can only be observed when an effort is made to accommodate as fully as possible, or when a persistent spasm of the ciliary muscles follows the introduction of physostigmine solution into the conjunctival sac. This effect, which was carefully investigated and explained by Hess (1897–99), is due to the fall of the lens by its own weight, towards either the nasal, the temporal, or the infra-orbital part of the ciliary body, according to the position of the head. The lens only remains centred and motionless in relation to the edge of the pupil when the head is held so that the plane of the iris is horizontal. At the least movement of the eyes to the sides the lens shifts in one direction or the other. This displacement can be accurately measured. Hess found that it may vary from 0·25 to 0·30 mm. in forced voluntary accommodation, and as much as 1 mm. in physostigmine poisoning.

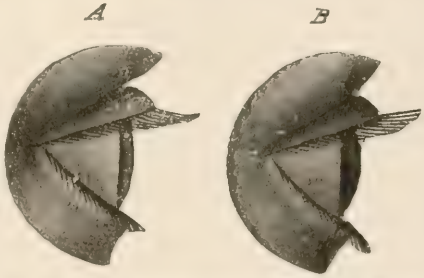


FIG. 133.—To show forward displacement of pupillary margin of the iris during accommodation. (Helmholtz.) *A*, profile view of eye in distant vision; *B*, in accommodation for near vision.

A further effect can be seen during accommodation, or after applying physostigmine, in eyes of which the iris is partially defective, owing to iridectomy or trauma. According to the accurate observations of Hess such eyes show during accommodation a bulging of the ciliary processes towards the equator of the lens without any thickening, a fact that can only be explained by assuming that in accommodation or in physostigmine poisoning the ciliary muscles move forward in the direction of the cornea. This is in agreement with the experiment of Hensen and Völkers (1873), who ran a very fine needle into the equator of a freshly enucleated human eye, and applied electrical stimulation near the ciliary processes — the needle then moved in a manner that indicated a forward displacement of the choroid. If the needle

was run into the ciliary bodies or near the posterior pole of the eye, no movement was visible.

These facts together show that accommodation is brought about by contraction of the ciliary muscle. Whatever the direction of its fibres—meridional, radial, or circular—the resultant of their contraction is the displacement forward towards the cornea, and backward towards the axis of the eye, of all the component parts of the ciliary processes. The first effect is due particularly to the

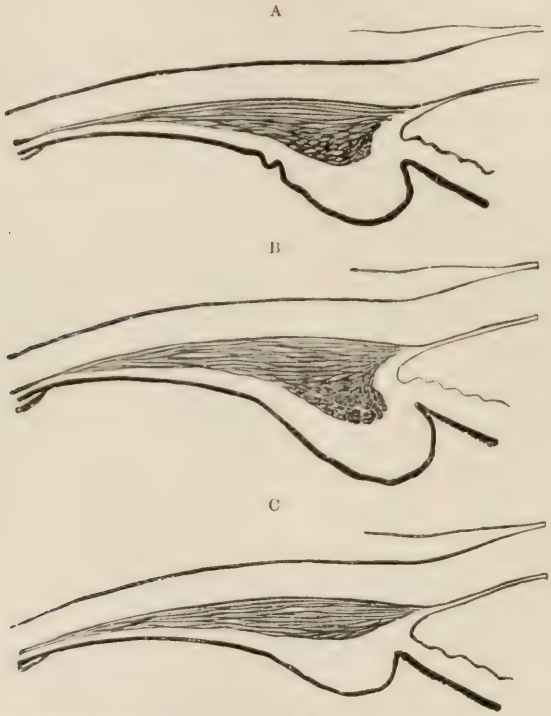


FIG. 134.—Comparative development of the circular fibres of the ciliary muscle in A, normal or emmetropic, B, hypermetropic, C, myopic eye. (Fuchs.)

meridional and radial fibres, the second to the circular fibres. According to the anatomical observations of Ivanoff (1869) the circular muscle-fibres are strongly developed in hypermetropic, and atrophied and almost absent in myopic eyes (Fig. 134).

This is borne out by the fact that hypermetropics are forced to keep their accommodation constantly active, while this is less frequently the case in emmetropia and seldom and in much less degree for myopia.

How does the contraction of the ciliary muscle effect the curvature of the lens? Various theories have been put forward,

among which that of Helmholtz is almost universally accepted by physiologists and ophthalmologists.

The lens, he says, is an elastic body which is kept radially extended during the relaxation of the internal eye-muscles, and is somewhat compressed by the traction of the zonule adhering to its border. During contraction the tension of the zonule and its peripheral traction on the lens cease, and the lens then contracts in the direction of its transverse diameter, and its axis lengthens. This necessarily increases the curvature of its two surfaces.

Mannhardt (1850) and Schön (1885) attempted to oppose this theory of *distension* or *relaxation* by the hypothesis of *increased tension of the zonule*. According to these authors it is more particularly the circular fibres and in a less degree the internal radial fibres of the ciliary muscle that contract in accommodation. In consequence of this contraction the ciliary processes are pulled inwards and backwards, and the anterior ligaments of the zonule are stretched and drawn back, causing increased curvature of the lens, diminished hydrostatic pressure in the anterior chamber, and increased pressure in the vitreous body. According to Tscherning (1897), on the contrary, the contraction of the deep layer of the ciliary muscle must draw the zonule backwards and outwards; at the same time the superficial layers of the ciliary muscle pull the choroid forward and prevent the retraction of the lens. This causes the peripheral zone of the lens to flatten, and its central and denser portion becomes more concentrated.

The later observations of Hess have established the arguments of Helmholtz. The appearance of lateral oscillations in the lens on forced accommodation, and the fact that after iridectomy the ciliary body is pushed forward during accommodation, are conclusive proofs of the earlier theory, while they contradict that of Schön and Tscherning.

Fig. 135 shows in a diagram the total mechanical effects which result from the contraction of the different parts of the ciliary muscle, according to the exhaustive observations of Hess.

The ciliary muscle is innervated by the oculo-motor nerve. The fibres that regulate accommodation issue from the anterior mesial nucleus of this nerve. On electrical stimulation of this nucleus Hensen and Völckers (1878) obtained accommodation in dogs.

The fibres of the oculo-motor that serve accommodation terminate in the cells of the ciliary ganglion; from this ganglion other fibres are given off to form the short ciliary nerves, which penetrate between the sclera and choroid to reach the ciliary muscle. Electrical stimulation of the separate short ciliary nerves produces bulging of the choroid and displacement of the lens for about 0·5 mm. (Hensen and Völckers). After poisoning with nicotine, artificial stimulation of the trunks of the oculo-motor

and short ciliary nerves of cats and rabbits no longer produces any effect of accommodation (Langley and Anderson, 1892). As it has been proved that nicotine paralyses the nerve-cells of ganglia, while it leaves the excitability of the fibres unaffected, this experiment proves that the cells of the ciliary ganglion are intercalated in the peripheral fibres that innervate the ciliary muscle (Vol. III. p. 367 ff.).

In normal eyes the innervation of the ciliary muscle is always synchronous and equal in both eyes, and extends to every part of the muscle. The question whether under special conditions unequal or unequally extensive accommodation in the two eyes is possible is of great practical interest, because it is conceivable that such an unequal innervation of the two sides might compensate a different refractive power in the two eyes. Schneller and A. E. Fick believed it possible to read very small writing with

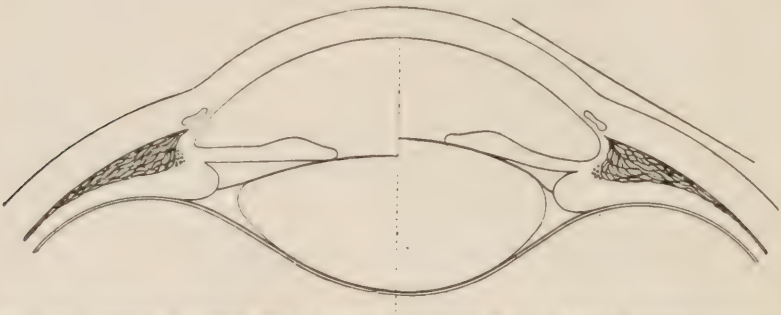


FIG. 135.—Diagram of anterior part of the eye, accommodated on the left for distant vision, on the right for near vision. (Luciani.) The figure shows that in accommodation the ciliary muscle thickens, the ciliary processes advance and approach the equator of the lens without increasing in size, the anterior and to some extent the posterior curvature of the lens increases, the sphincter of the iris contracts, the iris angle becomes more obtuse, and the anterior chamber is reduced in size.

both eyes, even when a *plus* or *minus* lens of more than 1 D. was held in front of one eye. But the later researches of Hess and Neumann (1892) make this hypothesis untenable. They found that normal eyes are notable by unequal accommodation to compensate an artificial difference in refraction amounting only to 0·12 D. And on the other hand, recent ophthalmic literature affords sufficient grounds for the belief that in cases of unequal refraction of the two eyes (*anisometropia*), and also in cases of *strabismus* and *unilateral blindness*, the accommodation in both eyes is equal.

The statement of Morat and Doyon (1891) that the sympathetic inhibits accommodation and serves to adapt the eye to distant vision has been contradicted by all the subsequent observers who have controlled it (Langley and Anderson, Hess and Heine, Römer and Dufour).

Accommodation is always associated with constriction of the pupils and convergence of the eyes. The first depends on the contraction of the sphincter of the pupil, the second on the contraction of the internal recti muscles, which are also innervated by the oculo-motor nerve. This functional association shows that there is a co-ordinating centre which simultaneously innervates the ciliary muscle, the sphincter of the pupil, and the internal recti muscles of both sides.

The associated contraction of the ciliary muscles and the recti interni is not inseparable. It is possible with a definite amount of convergence to alter the degree of accommodation, and with a constant degree of accommodation to vary the amount of convergence of both eyes within certain limits. This dissociation is easily effected by placing prisms or lenses in front of the eyes. If an object 30 cm. distant is focussed with both eyes and a concave lens of 4 D. is then brought in front of the eyes, a greater effort of accommodation is naturally required in order to see this object at the same distance; this is easily effected without producing double vision (*diplopia*), as would result if the increased contraction of the ciliary muscle were associated with increased contraction of the recti interni. If, on the other hand, convex lenses of 2·5 D. are brought in front of the eyes the contraction of the ciliary muscle must be decreased in order to see the object clearly, although the convergence of the two visual axes is maintained for 30 cm. distance, so that the contraction of the recti interni is not altered.

VI. Accommodation is confined between definite limits, within which alone distinct vision of an object is possible: a *near point* and a *far point* are to be distinguished.

The *near point* is that distance at which, with maximal curvature of the lens, the formation of a sharp image on the retina is still possible. According to Hess, it is not necessary for the production of the greatest lens curvature that the ciliary muscle should be in maximal contraction, since a moderate degree of contraction suffices. The correspondence between the near point of distinct vision and the maximal contraction of the ciliary muscle, as assumed by many, after Helmholtz, is therefore erroneous.

The *far point* of distinct vision is that point in space at which the eye is accommodated with the least possible curvature of the lens; this probably does not correspond with complete inactivity of the ciliary muscle (Hess). The distance between the near point and the far point was termed by Donders *range of accommodation.* Within this range the degree of accommodation, *i.e.* increase of lens curvature, is greatest at the near point, least at the far point, and increases gradually from the near to the far point. This is the logical deduction from the preceding argument on the

mechanism of accommodation, and agrees perfectly with the common observation that in looking at a distant object the eye (more exactly its musculature) is at rest; on looking at near objects the eye is at work, and easily becomes fatigued.

The range of accommodation diminishes regularly with age, as shown by the following table (Donders):

Age in years.	Range of accommodation in dioptres.	Age in years.	Range of accommodation in dioptres.
10	14	45	3·5
15	12	50	2·5
20	10	55	1·75
25	8·5	60	1
30	7	65	0·75
35	5·5	70	0·25
40	4·5	75	0

This gradual decrease in the range of accommodation depends, according to Helmholtz, not on any gradual alteration of the ciliary muscle, but on a progressive variation in the elasticity of the lens, particularly of the capsule, which is due to age and is physiological in character. During development, and especially in senile involution, the lens progressively thickens, and this thickening and hardening advance regularly from the nucleus to the cortex. The depth of the lens, too, diminishes somewhat with age owing to a slight diminution of curvature on both its surfaces, while in old age the static refraction of the eye also suffers to a slight extent in comparison with what it was in youth.

The curtailment of near vision manifested in age by diminished power of accommodation is known by the Aristotelian term *presbyopia*. This is seen in all eyes, hypermetropic, emmetropic, and myopic. The first, which require greater accommodation, show the effects of presbyopia at an earlier stage: the last, *i.e.* "short-sighted" eyes, later and to a negligible extent. According to Donders, all who require convex lenses to read from type before the age of 40 are hypermetropic; all who can read comfortably without spectacles at 50 or 55 are myopic.

Special devices are employed to measure the *near* and *far* points of distinct vision on which range of accommodation depends. It is usual in determining the near point to show the subject a book with small letters and to measure the least distance at which it is possible to see letters, syllables, and words distinctly. This method is inaccurate, because it is not easy to state exactly at what point the outlines are sharply perceived, since this depends also on other factors—*e.g.* relative size of letters, difference of luminosity between letters and background, degree of contraction of sphincter of the iris, etc.

More exact measurements can be made with the optometers of Porterfield or Stampfer, which are constructed on the principle of Scheiner's experiment. This consists in looking at a pin at different distances from the eye, through two small holes in a card or metal plate, made so close together that they both fall within the diameter of the pupil. The pin appears single, with sharp outlines, even if only weakly illuminated, when it is at such a distance that its image falls upon the outer layer of the retina. When the distance is greater or less it no longer appears as one pin but as two, with rather blurred outlines due to diffusion circles, although still fairly distinct because they arise from narrow, luminous cones.

This physiological experiment can be diagrammatically reproduced with a biconvex lens, a screen with two holes, and a receiving surface on which the flame of a candle is projected. In Fig. 136, *ef* represent the two holes in the screen that corresponds

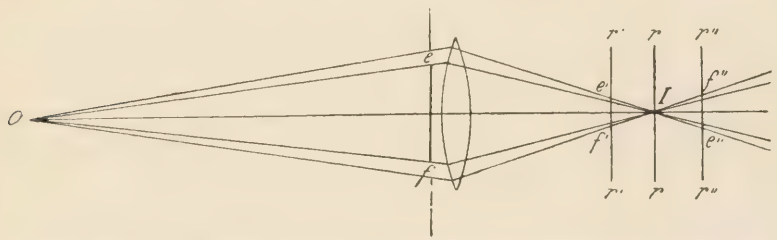


FIG. 136.—Diagram to illustrate Scheiner's experiment for determining the near point and far point of distinct vision, *i.e.* the range of accommodation.

to the pupil, *rr* the retinal plane on which the image *I* of the object *O* is projected. The image is single when the plane *rr* coincides with the seat of the image; when, on the contrary, it lies more in front (*r'r'*) or behind (*r''r''*) two images are formed, owing to diffusion circles *e'f' e''f''*. On closing hole *e* or *f* one or the other image disappears, either on the same or the opposite side, according as the double image is formed before or after the crossing of the rays. In experiments with the eye, owing to the image being inverted on the retina, the position of the images is the reverse of that in the figure, *i.e.* *e'* is below and *e''* above, or *f'* above and *f''* below.

Stampfer's optometer, constructed on the principle of Scheiner's experiment, serves principally for the determination of the far point. It consists of two tubes fitting one over the other like those of a telescope. One of the tubes which is brought close to the eye carries a convex lens of moderate focal length (8 D.), which makes the eye to which it is applied highly myopic, so as to place the mechanism of accommodation in complete rest. In front of this lens there is an opaque diaphragm

with two small holes or slits very close together. The opposite end of the second tube carries an illuminated slit in its centre. The inner tube is provided with a scale the middle of which corresponds to emmetropia. On looking through the instrument and varying the distance between the illuminated slit and the two apertures near the eye, it is easy to find the point at which a single image appears. The point of origin of the single image is the far point of clear vision, *i.e.* the static refraction of the dioptric system of the eye examined.

When the pupil is double, owing to congenital anomaly of the iris, double vision occurs (*monocular diplopia*) when the eye is not accommodated to the distance of the object; single vision when it is accommodated. In these cases the double pupil acts as an optometer.

Volkmann first endeavoured to determine how frequently in a given time he could accommodate the eye to the near point and far point, and came to the general conclusion that accommodation is rather a slow process; this agrees with the fact that it depends on the activity of smooth muscle fibres, which generally react slowly.

Hensen and Völckers found that accommodation for near vision takes place more slowly than for distant vision, showing that the contraction of the ciliary muscle is slower than its relaxation. Vierordt stated that accommodation for near vision required 1·18 sec., for far vision 0·87 sec. Aeby and Eilhard Schultze found that these figures varied considerably, but that the contraction of the ciliary muscle was always slower than its relaxation. Coccius obtained other results, and concluded that accommodation was more rapid for near than for distant objects; Schmidt-Rimpler gave approximately the same figures for both: 2·72 sec. for near vision, 2·44 sec. for distant. Angelucci and Auber, taking as their objective criterion the displacement of the image reflected from the anterior surface of the lens, in passing from near to distant vision, and *vice versa*, found no perceptible time-difference.

Donders observed that contraction of the pupils does not occur simultaneously with accommodation for near vision, but takes place a little later.

When the lens is absent (*aphakia*), either from a congenital anomaly or after an operation for cataract, the refractive power of the eye is deficient, *i.e.* there is a marked amount of hypermetropia, which can be corrected by a convex lens of 10-11 D. We have seen that this correction-value can be utilised to calculate the total refraction of the lens, although it comes out lower than is the case with other methods.

It has recently been maintained by a number of ophthalmologists that some degree of accommodation is possible, even when

the lens is absent. But the observations on which this statement are founded can be explained without assuming any power of accommodation. We pointed out that it is not indispensable to distinct vision that the posterior focal point should coincide exactly with the most external surface of the retina: it is enough if it falls within the mosaic membrane of rods and cones (the structure of which will be discussed below), which is about 0·06 mm. thick. Besides this we know that sight can be fairly clear when it is due, not to focal points, but to small diffusion-circles.

VII. Thus far we have considered the eye as a perfect optical instrument, as though the surfaces of curvature of its refractive media were quite spherical and perfectly centred, and these media completely homogeneous, transparent, and achromatic. More accurate observation of the eye, however, shows that from the dioptric standpoint it presents a series of imperfections or defects which are normally insignificant, but may under abnormal circumstances become so important as to interfere with vision. Taking these defects separately—

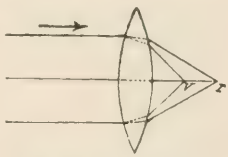


Fig. 137.—Chromatic aberration in an ordinary lens.

(*a*) Ordinary lenses break up white light, owing to the unequal refractibility or wave-lengths of the different coloured rays of which it is composed. This is known as *chromatic aberration*. Take for example a cone of parallel white rays falling on a convex lens (Fig. 137). The red rays, which are least refracted, unite at point *r* of the optical axis, while the violet rays, which are most refracted, converge at point *v*. Between these two extreme foci lie those of the intermediate colours, indigo, light blue, green, etc. If a diaphragm is inserted at point *r* a small white luminous circle bordered with a red line appears; if the diaphragm is introduced at *r*, the circle will be white with a violet edge. In both, the centre of the circles is white because a number of rays of different colours, which combine into white light, intersect there. The distance *vr*, comprised between the focal points of the extreme rays, may be taken as the measure of chromatic aberration.

This defect in common lenses can be avoided by the use of an *achromatic* lens, formed by the combination of two lenses (positive and negative) made of two substances with different refractive indices, so combined that they keep their power of convergence, while all trace of chromatic aberration disappears.

The eye has no achromatic system; its dioptric apparatus has different focal distances for rays of different wave-lengths. The focal point of the violet rays (Fraunhofer's *H* line) is nearer the lens than the focal point of the red rays (Fraunhofer's *B* line),

when the eye is accommodated to infinity. According to Wolf (1888) the distance between these two focal points (which indicate the degree of chromatic aberration in the eye) is 0·75 mm. According to Einthoven the distance between the focal point of line *D* (orange-yellow) and *F* (blue) is 0·27 mm. These values all relate to the schematic eye.

The diffusion-circle of a ray of red light has a diameter of about 0·1 mm. when the pupil is moderately dilated and the eye accommodated to violet light; the diffusion-circle for red and violet light is about 0·05 mm. in diameter when the eye is accommodated to rays of medium wave-length.

The following experiment is a convincing demonstration of the chromatic aberration of the eye. On looking at a distant flame through a cobalt-blue glass, which mainly allows red and blue rays to pass, the focal point of the red rays falls on the surface of the retina, that of the blue rays in front of it. In this case a red flame outlined with blue is seen. If, on the other hand, the flame looked at is close by, the focal point of the blue rays falls on the retina, and that of the red rays behind it. The flame now appears blue, outlined in red.

Under ordinary conditions we scarcely notice the chromatic aberration in our eyes, proving that it is a very slight defect which does not perceptibly disturb the sharp outlines of the visual images. The iris, by reducing the section of the cone of light that enters the eye, undoubtedly acts as a diaphragm and diminishes chromatic aberration.

(*b*) Another error common both to the eye and to lenses with a spherical surface depends on the fact that the homocentric rays, *i.e.* such as start from any given point, have, even when monochromatic, a different focus according as they are more or less central or peripheral. The rays nearer to the optical axis, or falling on the central part of the lens, are less refracted; the more eccentric rays, falling near the edge of the pupil, are more refracted. So that the rays of the homogeneous luminous cone which enter the eye, or spherical lenses in general, converge not in a *focal point*, but in a *focal line*. This is known as *spherical aberration*. It can be avoided in artificial lenses by altering their curvature so that it decreases gradually from the central point to the edge of the lens. It was formerly believed that the spherical aberration of the eye was partially compensated by the fact that the cornea exhibits the highest degree of curvature at its centre, and is somewhat flattened at the edge. But Auber and Gullstrand showed that the *optic zone* of the cornea, *i.e.* that which serves for vision when the pupils are of normal width, is not less curved at the periphery than at the centre. Only when the pupil is artificially dilated by atropine can it be assumed that the somewhat flattened peripheral corneal zone which then

comes into play renders the aberration rather less than it would be with perfectly spherical curvature of the cornea.

Under normal conditions spherical aberration is reduced by the iris which checks the penetration of the more oblique incident rays. Artificial limitation of the section of the luminous cone that enters the eye, obtained by holding a card with pin-holes in front of the eye, makes it possible — as shown on p. 292—to read printed characters, even when they are placed within the near point of distinct vision. This is explained not only by the reduction of the diffusion-circles, but also by the correction of spherical aberration.

According to Gullstrand the difference of refraction in the rays entering at the vertex of the cornea and at the margin of the optic zone is quite four dioptres. This degree of spherical aberration shows plainly that it depends not merely on the cornea, but, to a certain extent, on the lens as well.

(*c*) When the curvature of the visual zone of the cornea is examined it is found never to be really the segment of a sphere, but rather a segment of an unequal ellipsoid. Sections of the eye along the vertical and the horizontal axes do not give equal curves of intersection, but the vertical meridian almost always shows more pronounced curvature and the horizontal less.



FIG. 138.—Placido's keratoscope.

Gullstrand (1896) invented a method for the exact determination of the curvatures of the cornea in the different meridians. He photographed the mirror images of the cornea and measured the photographic images under the microscope. For the test-object he selected a figure with concentric circles, the so-called keratoscope of Placido shown in Fig. 138, or quadrangular figures. The deformation of the mirror images is the starting-point in estimating the inequalities of the corneal curvatures. The distance of the circles of the keratoscope and their distance from the cornea being known, it is easy by measuring the deformations of the circles in the different meridians to calculate the varying asymmetry and irregularity of the corneal curvature.

Fig. 139 is a diagram of the results obtained by Gullstrand with this method of measuring the horizontal and vertical meridians of the eye. The two curves *A* and *B* show that in the cornea investigated (apart from the little irregularities due to the unequal distribution of the lachrymal fluid on the surface) there was appreciable asymmetry and unequal curvature in the horizontal and vertical meridians. The optic zone which corresponds to the pupil, and which alone functions in vision, presents

less marked differences of curvature than the peripheral zone, where a rapid flattening is shown in the curves, with a rapid fall in refractive power. Moreover, the curves of the horizontal and vertical meridians in the optic zone are not symmetrical in relation to the optic axis, and on comparing the two curves it is seen that refraction is more uniform in the horizontal than in the vertical meridian. Gullstrand concludes that the visual zone of the corneal surface has a transverse-oval shape. As shown by the two curves it extends from the visual axis nasalwards for about 20 , outwards for about 25 , upwards 15 , downwards 20°. He believes that the rapid flattening of the vertical meridian is in relation to the pressure exerted by the eyelids on the cornea.

Astigmatism depends on the different curvatures of the cornea in the different meridians, and means that the rays that fall on one meridian are more highly refracted and reunite earlier

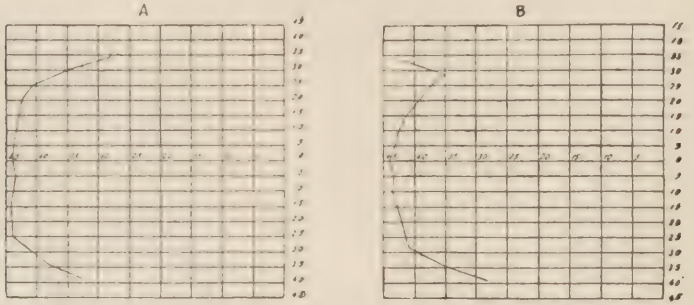


FIG. 139.—Diagram to show the curvature of the cornea (A) in the horizontal, (B) in the vertical meridian. (After Gullstrand.) The figures to the right of A and B show the angle formed by single points of the corneal surface with the visual axis ; the figures in the middle of A and B give the amount of refraction at the corresponding points of the two corneal meridia in dioptres. The irregularities of both curves are due to the unequal distribution of the lachrymal secretion over the surface of the cornea.

than those that fall on other meridians, *i.e.* have a different focal point. When the two meridians in which the focal distance reaches its maximum and minimum lie one vertically over the other, the astigmatism is regular. This form is very often present in so slight a degree that it produces no striking deformation of the retinal images.

The degree of astigmatism is expressed in dioptres, and is calculated as the difference in the static refraction of the two meridians in which refractive power is maximal and minimal.

According to the measurements made by Nordenson on young students of 7 to 20 years of age, in 452 eyes only 42, *i.e.* 9 per cent, showed no form of astigmatism. Astigmatism of more than 1 D. was present in sixty-four students ; of more than 1·5 D. in four. In the astigmatic eyes the most refractive meridian was in 85 per cent the vertical, only in 1·5 per cent the hori-

zontal, and in 13·4 per cent the oblique meridian. It is thus proved that in the great majority of cases the vertical is the most refractive corneal meridian, which bears out Gullstrand's view that the cause lies in the unequal flattening of the cornea by pressure of the eyelids.

In most instances, owing to ordinary corneal astigmatism, it is necessary, when looking fixedly with one eye at two black lines which cross on a white background, to bring the test-object a little nearer, in order to see the horizontal line distinctly, than is required in focussing the vertical. The eye is therefore comparatively myopic for horizontally, and hypermetropic for vertically placed objects.

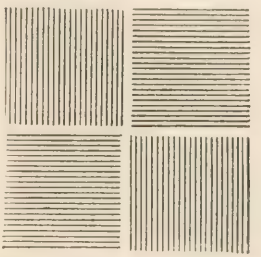


Fig. 140.—To illustrate the easiest method of detecting corneal astigmatism in the horizontal or the vertical meridian.

Various simple expedients have been proposed to facilitate subjective perception of astigmatism. One such, represented in Fig. 140, consists of four contiguous squares, two crossed by horizontal, two by vertical black lines at uniform distances. When the eye is accommodated for distinct vision of the horizontal lines, the vertical lines are less distinct; when it is accommodated for the vertical lines, the horizontal are blurred. Another method is shown in Fig. 141, which consists of equidistant, concentric circles. On looking at these circles attentively with one eye it is impossible to see all the lines in the different sectors clearly at the same moment; this is only possible in two opposite sectors, the position of which alters as the object is brought near or moved away, or when the degree of accommodation is altered. A third way of testing accommodation in one's own eyes is shown in Fig. 142, which consists of a number of concentric radii. If the figure is placed at such a distance from the eye that only the horizontal line is seen clearly, then on slowly bringing it nearer the oblique lines become plainer till finally the vertical line alone is seen distinctly, all the rest being more or less blurred.

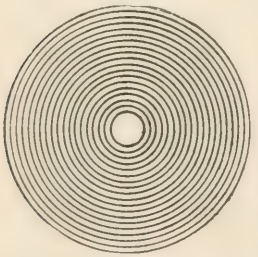


Fig. 141.—To demonstrate astigmatism in the different parts of the cornea.

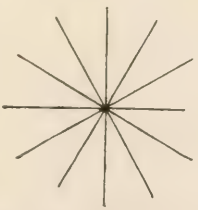


Fig. 142.—Illustrates how best to distinguish differences in corneal astigmatism in the different meridians.

Physiological astigmatism causes no appreciable disturbance of vision so long as it is slight, but when it exceeds certain limits, and becomes abnormal, it alters the shape of the retinal

images. It can be corrected by cylindrical lenses of such a strength that the asymmetry of the corneal curvature is compensated, *i.e.* the refractive power of the horizontal meridian, or of that meridian in which the refractive power is lowest, is increased. When the correction is perfect, the degree of astigmatism of the cylindrical correction-lens is equal to the degree of astigmatism in the eye.

(*d*) Physiological astigmatism depends not merely on the asymmetry of the corneal curvature, but also on the fact that the optical axis does not coincide with the visual axis, and that the refractive surfaces of the different dioptric media are not perfectly centred. The visual axis runs inwards and slightly upwards, and strikes the fundus outside and a little below the optic axis. In Fig. 128 (p. 288), of Helmholtz' schematic eye, *FF'* is the optic axis, *AV* the visual axis. The angle formed by the two axes is about 4° to 7° in the horizontal meridian, about 3°·5 in the vertical. The rays that reach the eye along the visual axis have therefore an oblique course. Owing to this fact a cone of homocentric rays penetrating the eye in the horizontal meridian becomes slightly astigmatic, because it is more refracted than those which enter by the other meridians. It is therefore true that the slight degree of astigmatism which thus arises is over-compensated by the opposite astigmatism due to the asymmetrical curvature of the cornea.

Starting from the fact that the angle between the visual line and the optic axis of the eye is usually about 5°, Gullstrand calculated the influence of the oblique incidence of the rays in the visual axis of the schematic eye, and found that the focal line does not exceed 0·03 mm., and the resulting degree of astigmatism 0·1 D. These low figures sufficiently explain why the oblique incidence of the line of vision causes no sensible diminution of its acuity.

The greater the angle formed by the incident rays with the optical axis, that is, the more oblique their direction, so much the longer will be the focal line, and so much the less clear the corresponding image on the retina. The farther the retinal image is from the centre at which the visual axis falls, and the more eccentrically it lies on the retina, the more blurred will it be. We shall deal more fully with these effects in examining *indirect vision*, which depends on the peripheral region of the retina.

The astigmatism due to oblique incidence of the rays may also be due to imperfect centring of the curvature of the different refractive media of the eye, because in this case again the rays which fall parallel to the axis or perpendicular to the first surface may fall obliquely on the other surfaces. Observations can be found in ophthalmic literature to show that even in normal eyes imperfect centring of the surface, as of the pupil, may be present,

independently of the drop of the lens during forced accommodation. But in any case the defect is very small and produces no perceptible visual disturbance.

To demonstrate the existence of astigmatism not due to asymmetrical curvature of the cornea, it is necessary to eliminate the influence of the latter by looking through water. Under water the human eye becomes extremely hypermetropic, because no reflection takes place at the surface of the cornea. In fishes the hypermetropia is compensated by the marked curvature of the lens, which becomes spherical. For man to see plainly under water a biconvex lens of about 28 D. is required, or (as Dudgeon proposed) a concave lens of air, made of a watch-glass applied to the eye in a water-tight tube. If vision under water through this correction-lens does not eliminate the astigmatism, it probably depends on defective centring or on an obliquity in the lens.

(*e*) Another common defect of the dioptric apparatus (present, according to Johannes Müller, in most individuals) is the so-called monocular polyopia (monocular diplopia or triplopia). This consists in seeing double or even triple images of an object with one eye, under certain conditions.

Monocular polyopia is independent of ametropia of the dioptric apparatus, since it can be observed both in myopes and in hypermetropes.

In the author's own case monocular diplopia and triplopia occur as follows. When looking with either eye without corrective lenses for presbyopia at black lines arranged as a cross, or as radii of a circle, traced on a white card (Fig. 142), double, treble, or even quadruple images of each line are seen, especially of those in certain planes, according to the degree of illumination, the distance of the card, and the rested or fatigued state of the eye. The multiple images are approximately parallel, and vary considerably in distinctness, one being sharper, the next less distinct, and so on. Their apparent distances are not equal, as the transverse or oblique lines seem more distant than the vertical. On looking at the figure with either eye through a correction-lens and at the proper distance, all the radii appear single, though more or less sharp or blurred according to the physiological astigmatism; only when the card is brought nearer, or moved beyond the limits of accommodation, do the images of all the lines appear double. Finally, on looking at the figure, with or without correction-lenses, through a pin-hole in the card (stenopaic diaphragm) the lines all appear single and equally distinct, whether the figure is brought close to, or moved away from, the eye.

These observations prove that monocular polyopia is due to *diffusion-circles*, since it entirely disappears when the objects are sharply focussed. To account for the phenomenon it is necessary

to understand how the blurred but single image seen when the retina is stimulated by diffusion-circles may split up into two, three, or four images of decreasing intensity and distinctness.

Johannes Müller did not attempt to give an adequate explanation of monocular polyopia. "These phenomena," he writes, "are due to the construction of the eye; in all probability they depend on the different systems of fibres of which each layer of the lens is composed."

Brücke suggested that the phenomenon might be due to spherical aberration of the surfaces of the dioptric mechanism; but he failed to demonstrate this, or to formulate any adequate theory.

Bull referred it to the unequal refraction of the various sectors of the lens. But this assumption was confuted by Verhöff (1902), who first offered a correct explanation of monocular diplopia,

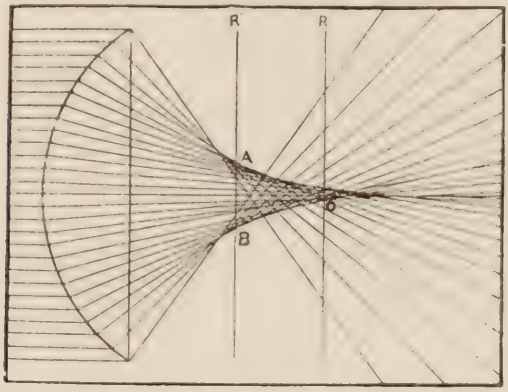


FIG. 143.—Construction to show refraction of parallel rays that pass through a lens with a spherical surface. (Verhoff.) Explanation in text.

which he found in many cases of astigmatism, by demonstrating that it could be reproduced in a photographic camera with a round lens, or better, a positive spherical lens uncorrected for spherical aberration, arranged with a stenopaic slit. Under conditions of hypermetropic refraction a double image of the luminous point is formed on the screen. He accordingly ascribed the phenomenon to astigmatism, associated with ordinary spherical aberration of the human lens. Inspection of Fig. 143 will explain this. Here the cone of parallel rays coming from a luminous point at infinite distance is refracted on passing through a denser medium limited by a spherical surface. The normal ray, *i.e.* that which cuts the principal axis of the lens, is not deflected; but all the other rays are more refracted in proportion as they are farther from the centre and nearer the periphery of the lens, *i.e.* as the angle of incidence at which they penetrate the spherical surface of the lens is greater.

When the screen is at *R*, at the focal point of the lens, almost all the rays fall on it close to the principal axis, at *O*. But if the screen is brought in front of the focus, at *R'*, the refracted rays form a diffusion-circle represented by *AB*. A glance at the figure, however, shows that they cannot in this case be distributed uniformly over the entire surface of the diffusion-circle; many of the rays fall on the periphery of the circle (at *A* and *B*), while very few cut the centre of it. The diffusion-circle is therefore seen as a ring that is brighter at the periphery than in the centre.

If the cone of light is now replaced by a line of light (by means of a stenopaic slit), the image thrown on the screen appears as a line with luminous points at the two extremities (*A* and *B*) and is not doubled.

M. Besso (1912), on throwing the image of a bright line on a screen with a lens of 10-12 D., and then bringing the screen in front of the focal point of the lens, saw the image of the line become simple. The phenomenon is explained by the superposition of the more luminous parts of the diffusion-circles that form the image of the line.

Spherical aberration in the dioptric system of the human eye is always associated, as we have seen, with a certain degree of astigmatism and imperfect centring of the dioptric media; the course of the refractive rays is consequently less simple, and the diffusion-circles are more complicated, according to the position of the rays. This explains why the phenomena of monocular polyopia present individual differences, and why some people see the line double, others triple, etc., under the above conditions. But the determining cause is stimulation of the retina by diffusion-circles.

(*f*) Owing to the fact that the refracting media of the eye consist partially of tissues formed of cells, it follows necessarily that they are not perfectly homogeneous and transparent. The rays of light that pass through them must undergo a certain amount of dispersion, but under physiological conditions this is not sufficient to blur the outlines of the retinal images.

There may also be more or less circumscribed and diffuse opacities in the different media, but these do not interfere with the function of the eye so long as it is accommodated to distant vision. They throw no shadow on the retina, but make the image less luminous. They can be entoptically perceived as dark spots when a card with a small central aperture, through which the light of a candle penetrates, is placed in front of the eye at the anterior focal point (about 13 mm. from the cornea). The rays of the pencil of light that reaches the eye from the illuminated aperture arrive at the retina in a parallel direction after refraction. Under these conditions the shadows of the opacities are projected

on the retina and are perceived as dark spots in the field of vision. If the light is moved in different directions in the same plane, the dark spots in the visual field also move, in proportion to their distance from the retina.

The larger opacities, which are never absent under physiological conditions, are cast by the rich vascular network formed in the inner layers of the retina by the central vein and artery. As this vascular network lies in front of the external sensitive layer of the retina, it would seem natural that we should normally be aware of the shadow projected by it. But under ordinary conditions this is not so. Helmholtz explains this fact by assuming that in the parts of the retina that are shadowed by vessels retinal sensibility is greater and its excitability less exhausted in comparison with the other parts that are not shaded and are therefore more influenced by light.

But when the eye is illuminated so that the shadows of the vessels are displaced and projected obliquely on to spots that are not shaded in the ordinary passage of the light-rays, the vascular shadows are at once recognised, as Purkinje (1819) first observed. The simplest method of producing this effect is to illuminate one of the eyeballs, which is directed on a wall of the darkened room, and accommodated for distant vision, obliquely by a candle held near the temple, so that the light enters the eye through the sclerotic. After moving the flame up and down a few times, the inverted image of the whole vascular network of the retina is projected, highly magnified, upon the wall.

Under special conditions it is also possible to see the movement of the blood corpuscles in the capillaries of the retina (Boissier)—as on looking through a blue glass at the sun, with accommodation relaxed. Shining dots, like sparks, are seen to move in figures up and down certain set paths. According to His this phenomenon depends on the concentrated light projected upon the outer layer of the retina by the erythrocytes circulating in the capillaries of its middle layer. If a red glass is substituted for the blue, the effect disappears owing to the less absorption of this light by haemoglobin (Abelsdorff and Nagel).

VIII. We have seen that the contraction of the sphincter of the iris is associated with that of the ciliary muscle in accommodation. The pupil, like the diaphragm of a photographic camera or a telescope, intercepts the homocentric peripheral rays of a cone of light from the fixed point, and thus reduces chromatic and spherical aberration: it constricts the visual zone of the cornea and diminishes the astigmatic effects of its asymmetrical curvature. But the main function of the iris is to regulate the amount of light that enters the eye and obviate a glare, and thus enable the eye to function as a perfect camera obscura. As the term *refractive accommodation* is applied to the gradual change in the refractive

power of the eye brought about by the activity of the muscles of the ciliary body, the term *moderative accommodation* may be applied to the changes of the aperture of the pupil consequent on the alterations of tone of the iridic muscles.

The movements of the pupil are involuntary and unconscious reflex acts. Under normal conditions the pupils are of equal size, and react reflexly to different stimuli synchronously and identically.

The width of the pupil when the degree of illumination is moderate differs greatly in different people, particularly in relation to age. It is very narrow in the new-born; increases up to 6 years of age; at 20 attains a diameter of about 4 mm.; then grows increasingly less with age up to about 50, when it is usually 3 mm.; and in old age is once more of minimal diameter (Silberkuhl and Pfister). The pupil is a little larger in women than in men; in hypermetropic persons it is smaller, in myopes larger, up to the twentieth year than in emmetropes. These differences are independent of the colour of the pigment of the iris (Tange, 1902).

Reflex contraction of the pupil takes place—

(*a*) When the retina is excited by the incidence of light. It contracts in proportion to the intensity of the light and the extent of retinal surface illuminated. This reflex action of light is, up to a certain point, independent of the activity of the apparatus for accommodation. Even when distant objects are focussed, the pupils may be contracted (*myosis*) with the lids half-closed when the light is too intense. In the same way they may be dilated (*mydriasis*) even in focussing near objects, if the light is weak.

Contraction does not occur instantaneously but begins, according to Listing, 0·4-0·5 sec. after the incidence of light, and reaches its maximum about 0·1 sec. later. The flash-light photographs by Claude du Bois-Reymond (1888) showed that the pupil is enormously dilated in total darkness. It is therefore owing to the action of light that it is considerably contracted under ordinary conditions.

The reaction of the pupil to light is in direct ratio with the intensity of the source of light. According to a law formulated by Vervoot (1900) an object = 1, illuminated with an intensity = 4, produces the same degree of reaction in the pupil as would be produced by an object four times greater, but four times more weakly illuminated. The reflex must therefore depend on the amount of light and not on the extent of retinal surface illuminated.

According to Ovio (1905) the size of the pupil varies inversely with the square root of the intensity of the light. It has been disputed by different authors whether on increasing or diminishing the intensity of light the alterations in the width of the pupil

occur with less or greater rapidity. To clear up the question Ovio adopted a coefficient of pupillary dilatation, and found this coefficient to be inversely proportional to the intensity of light.

(*b*) The pupil, as we have seen, contracts reflexly when the eye is accommodated to vision of near objects, and when the eyes converge. In such cases accommodation (contraction of ciliary muscle) and convergence (contraction of recti interni) take place more rapidly than the contraction of the sphincter of the iris. The association of these three movements is not constant. According to Ovio the pupil may react to accommodation alone, that is, apart from convergence of the visual axes, or on convergence alone. The reaction of the pupil in consequence of convergence of the axes seems, however, greater than that which occurs on accommodation.

(*c*) The pupil is contracted during deep sleep, in the early morning, in epileptic attacks, and in other nervous diseases.

(*d*) Myosis further occurs in the early stages of chloroform narcosis, and at almost every stage of poisoning with physostigmine, muscarine, morphine, and other drugs known as *myotics*. It is difficult to be certain of the exact cause of the myosis in all cases. Hyperaemia or increased flow of blood to the vessels of the iris may induce it; in fact, if the aqueous humour is drawn off by paracenthesis of the cornea, myosis results (Hensen and Völckers).

Reflex dilatation of the pupil is produced by—

(*a*) Passage from light to darkness, or diminution of the intensity of light.

(*β*) Adaptation of the eye to distant vision, which depresses the tone of the ciliary muscle, and makes the two visual axes parallel.

(*γ*) Excitation of the nerves by any kind of stimulus that produces pain (Cl. Bernard, Westphal). According to Schiff and P. Foà, sudden, gentle, tactile impacts produce a transient mydriasis. The dilatation of the pupil that accompanies dyspnoea and great muscular exertion is probably due to the rhythmic and continuous stimulation of the sensory nerves. Even under normal conditions inspiration coincides with a slight pupillary dilatation, and expiration with a slight contraction (Vigoureux). According to certain observers (Hensen) minute oscillations in the diameter of the pupil are visible at each arterial pulse. But these effects are in obvious relation with the respiratory and arterial variations in the blood-pressure and the rate of blood-flow in the vessels of the iris, and have nothing to do with the pupil reflexes.

(*δ*) Psychical emotions, such as fear, surprise, and the like, are also accompanied by dilatation of the pupil.

(*ε*) Lastly, mydriasis occurs in advanced stages of chloroform narcosis and alcoholic intoxication, and as the effect of a number

of poisons, either introduced into the blood or injected into the conjunctival sac, including atropine, duboisine, daturine, etc. While the myotic poisons induce persistent accommodation of the eye to near vision, the mydriatic poisons accommodate for distance; in other words, the former produce a spasm, the latter a relaxation of accommodation and of the pupillary movements. Cocaine in small doses is a mydriatic, in large doses a myotic.

To sum up, it may be said that the aperture of the pupil both under normal and under abnormal conditions varies constantly, owing either to oscillations in the tone of its muscles or to oscillations of the blood contained in its vessels. Sometimes this normal dynamic state is so exaggerated that there is intermittent contraction of the pupil, known to ophthalmologists as *hippus*, which may be associated with an analogous state of the external muscles of the eyeball, known as *nystagmus*.

IX. The movements of the iris depend essentially on the activity of its muscles. The sphincter of the pupil forms a ring round the inner border of the iris which may vary in diameter, according to the state of its contraction, between 0·6 and 1·2 mm. The existence of the musculus dilatator pupillae was clearly established by the anatomical researches of Grunert (1898) and others, but it had previously been known from the physiological experiments of Langley and Anderson (1892) on mammals. They applied electrical excitation to a group of ciliary nerves, after exposing a small portion of the sclera near the corneal edge, and observed a local traction of the pupil outwards, due to the simultaneous radial contraction of the corresponding portion of the iris and sphincter. They also found that a bit of iris separated from the rest by two radial incisions contracted on exciting the corresponding nerves. In these experiments they ascertained by means of the microscope that the pupillary dilatation was wholly independent of the contraction of the blood-vessels of the iris.

There is thus no doubt that there are two muscles of antagonistic action in the iris. According as the one or the other predominates, there is myosis or mydriasis. When both muscles contract, the contraction of the sphincter predominates.

According to the observations of Laqueur (1898) the sphincter of the pupil is capable of very large excursions. The muscle fibre-cells of which it is composed may shrink to $\frac{1}{3}$th their length during contraction. These observations recall the experiments made by Grünhagen (1874) on the isolated sphincter of the iris of the rabbit and the cat, when a strip of the muscle was connected to a lever writing on a smoked drum. The experiment seems important, and has not, so far as we are aware, been controverted by other workers. The results may be summed up as follows:—

The sphincters both in rabbits and in cats react in the same way to the influence of the external temperature. They shorten when

the temperature exceeds certain limits, and lengthen when it drops. But if these muscles are electrically stimulated when they have almost or quite reached the maximal thermal contraction, their reaction is different.

The sphincter of the rabbit (whether atropinised or not) responds to each stimulation by a marked contraction, followed by a still more marked relaxation, which takes the writing-point below the original zero line. Not infrequently, on stimulating with strong induced currents, the muscle lengthens directly without any previous contraction. This is constantly the case on stimulating with strong galvanic currents.

The sphincter of the cat's pupil behaves somewhat differently. It is very difficult with galvanic excitation to obtain any contraction of it; generally it lengthens in proportion to the intensity of the stimulus. It is rare to find the elongation preceded by a small and transient contraction.

Grünhagen recognised that the lengthening of the sphincter muscle is not a fatigue-effect, and gave the name of *elongation* to this *active relaxation*—in agreement with the theory we have brought forward elsewhere (Vol. III. p. 30) to the effect that both contraction and expansion are the effects of two opposite physiological processes.

The fact observed by Steinach (1882) and fully confirmed later on by Guth (1901), that the sphincter muscle of certain animals reacts directly to light by contracting, is of physiological interest. Consequently it seems in every respect to be a muscle endowed with peculiar physiological properties and specific excitability.

The dilatator is quite distinct in its anatomical and physiological characters from the sphincter. According to Grynfeld (1899) it is a continuous layer of fibrils radially disposed in front of the pigment cells of retinal origin which cover the posterior surface of the iris. It seems to be a variety of contractile tissue, similar to smooth muscle tissue, from which, however, it differs by the fusion of its contractile substance into a continuous layer. Its physiological value is considerably less than that of the sphincter, as is admitted by all ophthalmologists.

The motor fibres that innervate the muscles of the iris are carried by the cerebral and the sympathetic nerves (Vol. III. p. 363).

The constrictor fibres of the iris run with the oculo-motor nerve. They pass thence to the ciliary ganglion, enter into connection with its cells, and run on in the short ciliary nerves to the sphincter of the pupil. The relation of the motor paths of the sphincter and of the ciliary muscle to the cells of the ciliary ganglion was clearly demonstrated by Langley and Anderson (1894). Yet the ciliary ganglion does not seem to be in any way a peripheral centre for its afferent and efferent nerves.

The dilatator fibres to the iris start from the ventral roots of the eighth cervical and first thoracic nerves; they run by the rami communicantes to the superior thoracic ganglion, thence to the inferior and superior cervical sympathetic ganglia, and enter into relation with the nerve-cells of the latter. The fibres that take origin from these, according to Langendorff, must be regarded as the peripheral dilatator fibres of the pupil; they run to the eye from the plexus cavernosus as the long ciliary nerves. From the superior cervical ganglion other dilatator fibres ascend to the Gasserian ganglion, unite with the ramus ophthalmicus of the trigeminus, and also penetrate the eye as long ciliary nerves, without coming into relation with the ciliary ganglion.

The results of experiments bear out this course of the motor paths to the iris muscles. Pourfour du Petit (1727) was the first who observed that section of the sympathetic caused contraction of the pupil as well as conjunctival hyperaemia. Biffi (1846) completed the experiment by demonstrating that excitation of the sympathetic produces dilatation of the pupil. Budge (1851–55) discovered the spinal origin of the dilatator fibres of the pupil (Vol. III. p. 352). Claude Bernard (1858) found that the cervical sympathetic contains vaso-constrictor fibres to the iris as well as vaso-dilator fibres; that the vaso-constrictor fibres separate from the irido-dilatators above the superior cervical ganglion, the first following the course of the carotid, the second uniting into a branch that joins the Gasserian ganglion. On exciting these nerves alternately, François-Franck (1884) obtained vaso-constriction and vaso-dilatation in the iris, and found that mydriasis precedes vaso-constriction. Other observations show that the dilatator fibres of the Gasserian ganglion unite with the ramus ophthalmicus, and after section of the latter stimulation of the cervical sympathetic no longer produces mydriasis (Budge, Waller, Bolay, François-Franck, and others). Lastly, Braunstein's experiments (1894) showed that after extirpating the ciliary ganglion mydriasis could be provoked, either by exciting the cervical sympathetic or by direct stimulation of the long ciliary nerves.

The irido-constrictor action of the oculo-motor was first pointed out by Herbert Mayo (1823); but it was reserved for Claude Bernard (1858–62) to demonstrate that "the fibres of the third pair of nerves become active after passing through the ciliary ganglion," and that stimulation of the intracranial branch of the oculo-motor has no effect on the sphincter of the pupil, while stimulation of the short ciliary nerves causes pronounced myosis. Kölliker and Michel (1894–96) found an anatomical connection between the fibres of the oculo-motor and the cells of the ciliary ganglion, from which the constrictor fibres for both the sphincter of the pupil and the ciliary muscle are derived. Apolant (1896) confirmed this, and observed that after section of the third nerves

in the cat, which has a large ciliary ganglion, Marchi's method shows no degeneration of the fibres of the ciliary nerve.

The immediate centre for the constrictor fibres of the pupil is the nucleus of the oculo-motor nerve. By exciting this in dogs, Hensen and Völckers (1878) found that it lay behind the centre for the ciliary muscle, which contracts on accommodation.

The centre for the dilatation of the pupil lies in the lower part of the cervical cord (Steil, 1894).

Both centres are normally in tonic excitation, so that after section of the oculo-motor the pupil dilates, after section of the sympathetic it contracts. The tone of the constrictor fibres is mainly reflex, as it ceases after division of the optic nerve (Knoll); yet the pupillary myosis of sleep demonstrates the existence of an automatic tone as well. The tone of the dilatator fibres is predominantly automatic.

The tonic action of these centres is normally equally active on both sides. The reflexes aroused by light or darkness also take place simultaneously and equally in both eyes, even when the positive or negative stimulus affects one eye only. In this case the reflex that occurs in the non-stimulated eye is called *indirect* or *consensual*.

Garten (1897), in order to study the course of its reflex, photographed the pupil on sensitised moving paper, and succeeded in demonstrating that as the effect of darkness it dilated rapidly in the first 5 secs., then more slowly, and finally reached its maximal dilatation, at which it remained for several hours.

If, after being kept in the dark for a minute, the eye is suddenly illuminated by a magnesium flame, the pupil contracts after a latent period of about 0·5 secs., reaches the maximum of contraction in about 4 secs., remains stationary for 6 secs., and finally relaxes—at first rapidly and then more slowly. The contraction of the pupil is greater and more prolonged in proportion with the adaptation of the eye to darkness, *i.e.* with its sensibility to light.

Schirmer noted that in passing from darkness into an illuminated room the pupil at first contracts rapidly, then dilates slowly, and only resumes its normal size after two to four minutes. Garten further saw that a slow increase of luminous intensity, within certain limits, produces no change in the pupil, while a rapid increase of light to the same intensity causes marked pupillary constriction.

Bellarminoff, by the same photographic method as Garten, studied the dilatation of the pupil that ensues in animals on stimulating the sympathetic after dividing it (*direct dilatation*), and that consequent on stimulation of the central trunk of the sciatic or other sensory nerve (*reflex dilatation*). The two reactions are different in type, as appears from Figs. 144, 145. In the first

type the latent period is rather shorter, the dilatation of the pupil more rapid, and the return to its initial size is rapid at first, and then very slow and gradual. In the second type the latent period is longer; the initial dilatation is followed by sudden constriction at the close of the stimulation; then follows a secondary dilatation, which is more ample and prolonged; finally there is a slow and gradual constriction until the normal diameter is regained. This

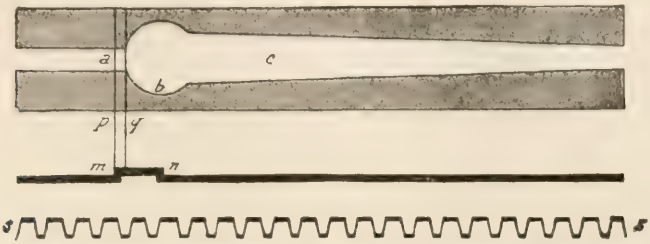


FIG. 144.—Diagram of direct pupillary dilatation. (After Bellarminoff.) *a*, pupil after section of the cervical sympathetic; *b*, maximal dilatation on stimulation of the sympathetic; *c*, progressive contraction till pupil recovers its original diameter; *m*, *n*, duration of electrical stimulation; *p*, *q*, latent period; *s*, *s*, seconds.

varying course of the pupil reaction is the external expression of the active intervention of the reflex centres.

How does the oculo-motor nerve produce myosis, and the sympathetic mydriasis? A definite answer to this question is not easy. If we consider the sphincter alone as the prevailing muscle of the

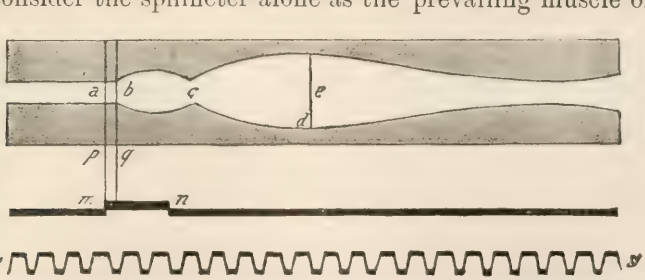


FIG. 145.—Diagram of reflex pupillary dilatation. (Bellarminoff.) *a*, pupil after section of sciatic nerve; *b*, primary dilatation during stimulation of central end of the sciatic; *c*, contraction of the pupil after stimulation; *d*, secondary dilatation; *e*, moment of maximal dilatation; *m*, *n*, duration of electrical stimulation; *p*, *q*, latent period; *s*, *s*, seconds.

iris it may be concluded that the oculo-motor—by means of the cells of the ciliary ganglion and the short ciliary nerves—causes the sphincter to contract, while the sympathetic—by means of the superior cervical ganglion and the long ciliary nerves—inhibits its tone, or causes active expansion. But in view of the anatomical and physiological evidence that the iris is also provided with a dilatator muscle, the action of which is antagonistic to that of the sphincter, one is forced to conclude that the oculo-motor and the sympathetic fibres have an opposite action upon the two muscles

—that the former contracts the sphincter and relaxes the dilatator, while the latter contracts the dilatator and relaxes the sphincter.

In explaining myosis and mydriasis some authors—particularly Grünhagen—have ascribed great importance to the vaso-motor nerves to the iris that accompany the ciliary nerves. They hold that independently of the variations in the tone of the muscles of the iris, vascular constriction and anaemia are capable of producing mydriasis, while vascular dilatation and hyperaemia may produce myosis. But this theory is contrary to certain definite experimental facts: (*a*) mydriasis may be produced by excitation of the sympathetic even when the vessels have been emptied by profuse bleeding, or the arteries of the neck tied; (*b*) the constriction of the iridic vessels obtained by excitation of the carotid fibres of the sympathetic above the upper cervical ganglion does not alter the diameter of the pupil (François-Franck); (*c*) the mydriasis consequent on excitation of the sympathetic is not synchronous with, but precedes, the constriction of the vessels of the iris (Arlt and others); (*d*) stimulation of the carotid fibres of the rabbit's sympathetic, which produces an obvious ischaemia of the iridic vessels, not merely fails to produce mydriasis, but even causes a slight degree of myosis (Angelucci).

The determination of the centripetal paths and centres for the constrictor and dilatator reflexes of the pupil is based particularly on clinical observations associated with anatomo-pathological discoveries.

The centripetal paths for the pupil reflexes that occur on stimulating with light are represented by the fibres of the optic nerve, which undergo partial decussation in the chiasma (Vol. III. p. 492). It is a remarkable fact that even when the chiasma has been divided in the median line in monkeys, not only the direct but also the consensual pupil reflexes are preserved (Bernheimer, 1898).

Clinical observations on disease of the terminal nuclei of the fibres of the optic nerve tend to show that the pupil reflex is served by optic fibres other than those which subserve vision.

In the mesencephalon, and particularly in the anterior corpora quadrigemina, the centripetal paths of the pupil reflex come into relation with the cells of the oculo-motor centre, and from there the centrifugal paths proceed to the sphincter of the pupil and ciliary muscle. According to Bernheimer, on the contrary, the optic fibres concerned in this reflex are directly connected with the oculo-motor nucleus, but the anatomical observations on which he bases his theory have not been confirmed by other authors. On the other hand, Bach and Majano, on the strength of other anatomical observations, hold that the optic fibres terminate in the anterior quadrigeminal bodies, and from these fibres pass directly into the oculo-motor nerve, unconnected with

the cells of its nucleus. But in order to explain the normal association of pupillary contraction with accommodation due to contraction of the ciliary muscle and convergence of the visual axes produced by contraction of the recti interni, it must be assumed that the centres of these reflexes lie close together and are probably all contained within the nucleus of the oculo-motor nerves.

To account for the co-ordination that exists between myosis and mydriasis (pupillary constriction and dilatation) it must be assumed that from these reflex centres, whether they be in the corpora quadrigemina or in the nucleus of the oculo-motor nerves, paths run into the cervical cord, and come into connection there with the cilio-spinal centre, and that on their activity depends the contraction of the dilatator muscle and the active relaxation of the sphincter of the pupil. Anatomical research has not, however, discovered the course of these internuclear paths.

Besides the peripheral centres, and those lying in the cord, medulla oblongata, and mid-brain, it is necessary to admit the existence of cortical centres, both for myosis and for mydriasis.

The cortical centres for contraction of the pupil lie in the occipital lobe, in the second external convolution in rabbits and dogs. On gently stimulating this area with the faradic current, transitory contraction of the pupil results (Bechterew, Plitz, Angelucci). The cortical centres for dilatation of the pupil lie in the sensory motor area. Ferrier, Katschanowski, Hensen, and Völckers hold that this cortical centre, which when stimulated produces mydriasis, is the point of origin of the cervical sympathetic. Grünhagen, Bochefontaine, and Braunstein, however, found that mydriasis may occur even when the cervical sympathetic has been divided. Angelucci confirmed this, but noted that the reflex is abolished immediately after section of the sympathetic owing to the inhibition produced by traumatism.

X. To avoid blurring of the outlines of images projected on the sensitive plate of a photographic apparatus by the diffuse light reflected from the walls of the camera, the latter is usually painted black. In the eye sharpness of the retinal images is obtained by the layer of black pigment that clothes the outer surface of the retina and extends from the posterior pole of the eye to the iris, and by the pigment of the uvea. Albinoes, who have no retinal and uveal pigment, are dazzled even by moderate light, and are consequently forced, in focussing illuminated objects, to close the eyelids so as to leave only a narrow slit between.

The pupil of an albino looks red, though the normal pupil appears black. From this it seems logical to conclude that under normal conditions the pigment of the retina and uvea absorbs all the light that enters through the pupil, and that it is only when there is no pigment that it is possible to look into the fundus of

the eye. This was in fact the theory put forward by Boerhaave and supported by Haller. But it is based upon an erroneous interpretation of the facts. The fundus of the albino eye looks red, not owing to absence of pigment, but because the light penetrates not only through the pupil, but also through the sclerotic and uvea, which are semi-transparent. Donders found, on placing an opaque diaphragm with an aperture of the same diameter as the pupil in its centre in front of an albino eye, that the pupil appeared black, as in normal pigmented eyes. The fundus of the pigmented eye accordingly looks black because it is not sufficiently illuminated, as light can only enter by the pupil, and the light that enters and is not completely absorbed by the pigment leaves in the same direction as that by which it entered, and may consequently be intercepted by the head of the observer.

Another argument against Boerhaave's theory is that the eyes of many carnivora and nocturnal animals glitter in the dark. To explain this it was assumed that the fundus of the eye in these animals was phosphorescent like the photogenic organs of certain insects, and served as a lantern to detect their prey. It was also stated that this photogenic activity of the retina increased if the animals were irritated.

Prévost of Geneva (1810) first discovered the true explanation of this phenomenon. He proved that the scintillation in the eye of the dog, cat, etc., is due to the light reflected from the *tapetum cellulosum* with which the fundus of the eye in these animals is provided, and which acts as a mirror. The shimmer is never seen in total darkness, but only in twilight, and it cannot be provoked by the will nor by external stimuli.

Gruithuisen confirmed the observations of Prévost, and added the fact that the shining of the pupil may persist in dead animals. The retina, therefore, has no photogenic power, and the phenomenon depends on the light from without, which penetrates the eye and is reflected from the fundus.

As early as 1704, Mery observed that it was possible under certain special conditions, as on examining an eye after placing the head under water, to distinguish the vessels of the cat's retina in full light through the pupil. In 1709 the celebrated geometer and astronomer de la Hire, commenting on Mery's observation, demonstrated that immersion in water abolishes corneal refraction and apparently brings the fundus of the cat's eye nearer the eye of the observer. The view of the retinal vessels is facilitated, as the pupils dilate in consequence of immersion and the fundus is better illuminated. These important observations of Mery and de la Hire long remained barren, and were not utilised as the starting-point of the practical problem of ophthalmoscopy, that is how, under ordinary conditions, to obtain a distinct view of the fundus of the eye, both in the lower animals

and in man. This problem was solved a century and a half later by Helmholtz (1851), after some preliminary attempts by Brücke.

Brücke noted that the human eye which has no tapetum can also, under certain conditions, reflect enough light to make the field of the pupil appear red. The eye must be illuminated in a dark room by a light held sideways to the observer's eye, and the observed eye must not be accommodated to the light. The

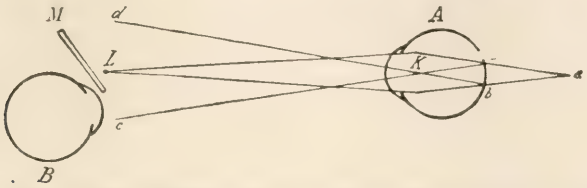


FIG. 146.—Diagram to show Brücke's method of seeing the illuminated fundus of the eye.

diagram (Fig. 146) shows the arrangement of the experiment. As the observed eye *A* is not accommodated to the luminous point *L*, a diffusion-circle *ab* is formed on the retina; the light is reflected from this diffusion-circle outwards in the form of a cone *cKd*, which has its nodal point at *K*. The observing eye *B*, which is near *L* and protected from the direct rays of light and heat by the screen *M*, is in the field of the cone of divergent rays issuing from *A*, and the pupil of the latter, therefore, appears red. It is obvious that the observed eye must be hypermetropic or myopic if the observer is to see it illuminated; an emmetropic (accommodated) eye which reflects the rays from the fundus in a parallel direction cannot be seen illuminated, because the observer is unable to bring his eye into the field of the reflected rays without intercepting the source of light with his head.

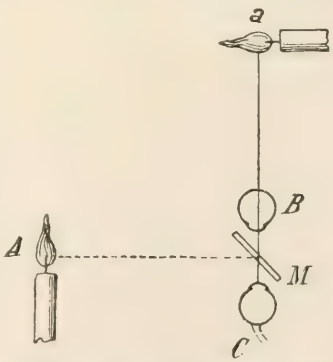


FIG. 147.—Diagram to show Helmholtz' method of seeing the illuminated fundus of the eye.

According to Brücke's observations, it was necessary, in order to see the fundus of an eye of any refractive power, to find a method of bringing the eye of the observer into the path of the rays reflected from the observed eye without intercepting the light that made it visible. Helmholtz succeeded in doing this in 1852. He illuminated the observed eye by light reflected from three superposed glass plates, through which he was able, owing to their perfect transparency, to see the fundus illuminated red, no matter what the refractive power of the eye, provided the pupil was sufficiently dilated to admit of adequate illumination.

The arrangement is shown in the diagram (Fig. 147): *C* represents the eye of the subject; *B* that of the observer; *M* the mirror consisting of one, or better three highly transparent glass plates; *A* the source of light. Part of the rays emanating from the flame are reflected by the glasses into the pupil of the eye *C*; the light reflected from the fundus of this eye passes through *M*, subjected only to a slight lateral displacement, follows the direction of the mirror image *a*, and reaches the eye of the observer *B*, on which he sees the pupil of *C* as a red field.

From the ophthalmologist's point of view it is important, however, not merely to see the fundus of the eye in a general way, but clearly to distinguish all the anatomical details of the retinal surface.

Theoretically this should be possible without artificial aid when both eyes are emmetropic and their accommodation entirely relaxed. In this case the parallel rays would unite in a focus on the retina, both of the observed and of the observing eye; then the one would distinctly see the fundus in the other, and *vice versa* (Fig. 148).

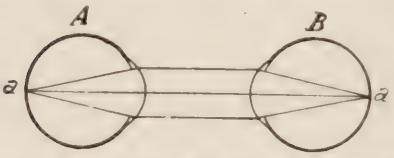


FIG. 148.—To demonstrate how two emmetropic eyes (when sufficiently illuminated with accommodation relaxed) can each view the fundus of the other.

Theoretically this is also possible when one eye is myopic and the other hypermetropic to a corresponding degree, and accommodation is relaxed in both, as the divergent rays from the hypermetropic eye are made sufficiently convergent by the dioptric mechanism of the myopic eye to come to a focus in the retina of the latter, or the convergent rays from the myopic eye may fall on the retina of the hypermetropic.

Finally, a distinct view of the fundus of an eye is theoretically possible in both emmetropic and ametropic eyes, when one or both are appropriately accommodated. But it is clear that in all these cases a distinct view of the fundus can rarely be obtained, because it is difficult to ensure that the one eye shall maintain such a state of complete repose or degree of accommodation as is required to give a distinct view of the fundus.

Helmholtz solved the practical problem of ophthalmoscopy by interposing between the observed and the observing eye a plano-concave lens, by which a magnified and erect virtual image visible to the observer can be formed. The ophthalmoscopic method, as first devised by Helmholtz, is shown in the diagram (Fig. 149). *A* is the observed, *B* the observing eye; *f* the flame, which is partially reflected on to *A* by means of the system of glass plates *ab* which acts as a mirror; *d* the correction lens, held nearer to or farther from *B*, according to the refractive power of the two eyes.

This optic system, consisting of the refractive media of the observed and observing eye, and a plano-concave lens, may be compared to Galileo's telescope, or to an opera-glass, which consists of an objective formed of a convex lens, and an eye-piece formed of a concave lens. The objective in Helmholtz' ophthalmoscope is represented by the dioptric apparatus of the observed eye, and the eye-piece by the concave lens placed before the eye of the observer. By regulating the distance of the two eyes in ratio with their refractive power, and by bringing the correction lens nearer to or farther from the eye of the observer, it is easy after a few experiments to focus so as to see the details of the retina distinctly. This is facilitated by selecting the concave lenses according to the

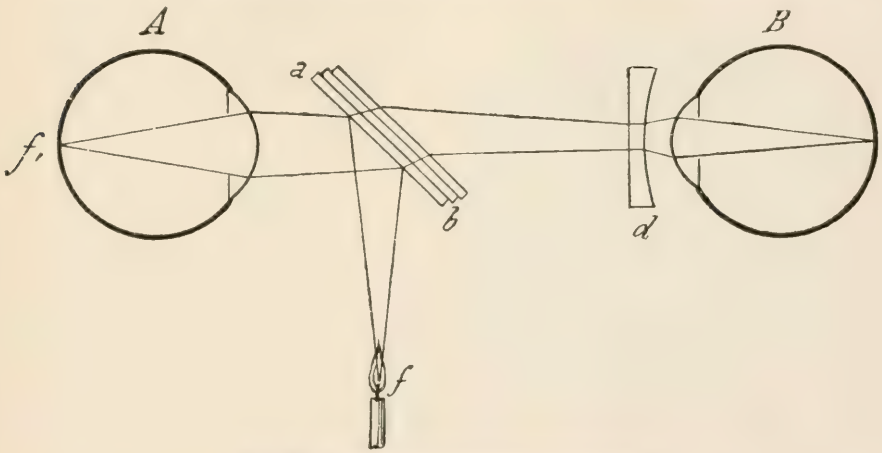


FIG. 149.—Diagram of Helmholtz' ophthalmoscope.

refractive power of the eye under examination—stronger (*plus*) for myopic, weaker (*minus*) for hypermetropic eyes.

Immediately after the invention of Helmholtz' ophthalmoscope, the celebrated oculist Rüte described another more practical method, based on the principle of Kepler's telescope, which is a system of convex lenses that form an inverted, magnified, real image of the object. Rüte first employed a concave metal mirror with a central aperture to illuminate the observed eye, instead of Helmholtz' glass plates. Hasner subsequently replaced the metal mirror by one of silvered glass, in which a central aperture alone was left transparent.

The principle of Rüte's ophthalmoscope is shown in Fig. 150. The source of light is placed to one side of the observed eye *A*; the mirror *M*, which reflects a large cone of light on to *A*, is placed somewhat obliquely in front of the eye of the observer *B*; a biconvex lens of medium focal length is held close to *A*, and by

its means the rays reflected from the fundus (no matter what the refraction of the observed eye) become convergent, and form an inverted image between the lens and the mirror. If the observer

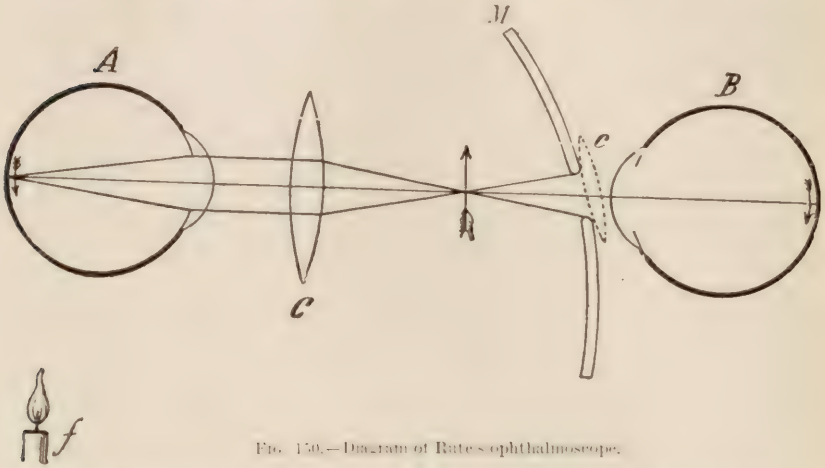


Fig. 150.—Diagram of Rate's ophthalmoscope.

is short-sighted, he is able to see the image without other aid; if normal or long-sighted, he is obliged, if his accommodation is not sufficiently powerful, to place a second slightly convex lens behind the mirror.



Fig. 151.—Ophthalmoscopic appearance of the fundus of the normal eye in a young person, with scanty pigmentation—the fovea centralis is plainly visible. (Uthoff.)

The first object in an ophthalmological observation is to see the papilla of the optic nerve distinctly. In order that it may come into the visual field of the observer, the observed eye must be turned a little inwards and its pupil dilated as much as possible.

The ophthalmoscopic image of the fundus of the normal eye exhibits all the details shown in colour (Fig. 151).

The optic papilla appears as a roundish or oval disc of pale pearly grey, which stands out sharply from the red colour of the rest of the fundus. From its centre issue the central artery and vein, which form a delicate arborisation over

the whole surface of the retina. The arteries are easily recognised by their brighter red colour, and by the stronger reflection of light from their surface. The hue of the fundus may vary from light-red to brownish-red, according to the amount of pigment it contains. Within physiological limits the appearance of the fundus varies considerably in different individuals.

Many attempts have been made to obtain a direct photograph of the fundus of the eye. Among the more recent are those of Fick and Gerloff (1891), Thorner (1896), Borghi and Bonacini (1898), Nicolaew and Dogiel (1900–1903), Bajardi (1905). But Dimmer (Graz, 1899–1904) alone succeeded in obtaining almost perfect photographs of the fundus by exposures of $\frac{1}{10}$-$\frac{1}{20}$ sec. (Fig. 152).

The most important part of the retina visible by the ophthalmoscope is the so-called *yellow spot* (macula lutea), which is distinguished by its lighter colour and absence of any visible blood-vessels. The yellow tint that gives rise to the name "macula lutea" is a post-mortem phenomenon which is not present in the freshly excised eye (Gullstrand).

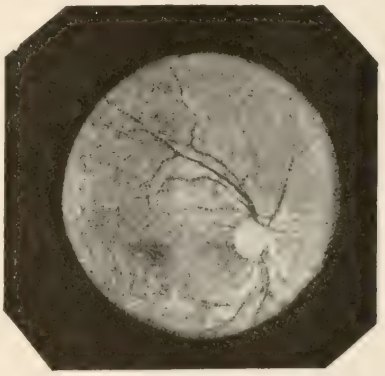


FIG. 152.—Photograph of fundus of normal eye in a man aged 38. Magnified about 4 times. (Dimmer.)

The elliptical yellow spot has at its centre a slight depression known as the fovea centralis. In the excised eye the diameter of the yellow spot is about 1-2 mm.; the fovea only from 0·2-0·4 mm. It is at this point that the image of the object which we focus is formed; in other words, the visual axis passes through the fovea. In fact, for the observer to see the yellow spot and fovea with the ophthalmoscope, it is only necessary that the observed eye shall be turned directly on to his.

Ophthalmoscopy not only enables us to ascertain the state of the fundus, but by it the static refraction of the eye can be more or less accurately determined.

We said that when the observer's eye is emmetropic he is able without a correction lens to see plainly the vessels in the eye focussed on a distant object; the eye investigated being also emmetropic. If it is necessary to add a correction lens to the ophthalmoscope, the observed eye is ametropic; if a concave lens is needed, it is myopic; if a convex lens, hypermetropic.

The degree of myopia and hypermetropia may be determined from the strength of the weakest lens required to obtain a clear

view of the fundus, if the distance between the correction lens and the observed eye is constant, the eye of the observer being always emmetropic and its accommodation relaxed.

But as a matter of fact perfect emmetropia is rare, and in near vision we are apt to make more or less use of our ciliary muscles, so that in determining static refraction by the ophthalmoscope it is also necessary to know the refraction of the observing eye. If $+x$ is the refraction of the correction lens, y the refraction of the observer's eye, r the static refraction of the observed eye, then $r = x - y$.

Ophthalmoscopy is not, however, the most practical, rapid, or certain method for the exact estimation of the static refraction of an eye. *Skiascopy*, invented by the French oculist Cuignet (1873-74), and developed by Leroy (1884) and Parent (1880-87), gives far more accurate results.

We have seen that when a pencil of light is thrown by an

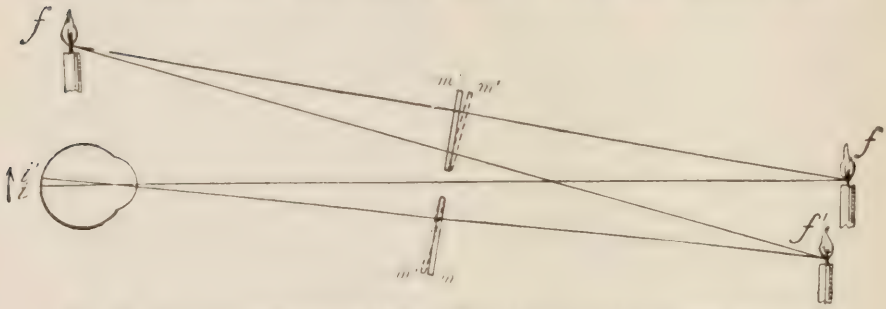


FIG. 153.—Displacement of the image of a flame reflected from a plane mirror into the fundus of the eye, by gently rotating the mirror round an axis passing through its central aperture.

ophthalmoscopic mirror into the pupil, the latter appears red. If the observer then rotates the mirror a shadow is seen to pass across the illuminated pupil from left to right, or from right to left, from above downwards or from below upwards, according to the direction of the movements given to the mirror. By the observation of these shadows the static refraction of the observed eye can be quickly determined.

Skiascopy is usually practised with a plane mirror. The observer places himself 1 metre away from the observed eye, into which he throws the beam of a lamp placed at the level of one of the subject's ears. On rotating the mirror round an axis passing through its centre, corresponding movements of the light rays and shadows in the pupil are seen. Fig. 153 shows that when the mirror moves from mm to $m'm'$, the virtual image of the flame is displaced from f to f', and the retinal image from i to i'.

The rays of light penetrate the observed eye as if they came from the reflected image, which—as the mirror has a plane

surface—is twice the distance of that between the lamp and the mirror.

The images are sharp when the image of the flame falls on the retina of the observed eye, if this is accommodated for distance. When the observer is 1 metre away from the observed eye and the lamp, the virtual image of the latter will be 2 metres from the eye under observation. If the subject can see the image plainly, there must be not more than 0·5 D. of myopia, otherwise the retinal image is more or less blurred, in proportion with the degree of ametropia.

When at the above distance a hypermetropic, emmetropic or slightly myopic (myopic by less than 1 D.) eye is examined, a shadow is seen in the pupil which, on rotation of the mirror, is displaced *in the same direction*, and vertical to the axis of rotation of the mirror. When, on the contrary, the observed eye is myopic to more than 1 D., and its distance point consequently lies nearer than the observer's eye, then the displacement of the shadow takes place *in the opposite direction* to the movement of the mirror, owing to the crossing of the rays that converge from the myopic eye to its far point. The first is known as the *direct*, the second as the *indirect* shadow.

To determine the degree of ametropia it is now only necessary to place a plus or minus correction lens in front of the observed eye, so as to transform the direct into an indirect shadow, or *vice versa*. The strength of this correction lens gives the degree of the myopia or hypermetropia. During examination, the accommodation of the observed eye must be absolutely relaxed; the observer's eye, on the contrary, must be accommodated to the plane of the pupil of the observed eye. The details of this method will be found in all recent text-books of ophthalmology.

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CHAPTER VII

RETINAL EXCITATION AND VISUAL STIMULATION

CONTENTS.—1. Histological structure of retina. 2. Direct and indirect vision (blind spot, retinal elements the receptors of light-stimuli). 3. Objective phenomena of retinal stimulation (visual purple, migration of pigment, contraction of epithelial cells and inner segment of cones, electromotive phenomena). 4. Colour vision; effects produced by different kinds of luminous radiation; limits of their visibility. 5. Visual acuity; phases of visual sensations; positive and negative after-images. 6. Retinal adaptation to light and darkness; sensibility of central and peripheral regions of retina to day vision and twilight vision (photopia and scotopia). 7. Achromatic and chromatic perceptions in relation to intensity of light stimulus and retinal adaptation to light and darkness. 8. Duplicity theory of functions of rods and cones. 9. Colour mixtures; complementary colours. 10. Colour contrast; successive and simultaneous. 11. Theories of achromatic and chromatic vision. 12. Colour blindness; partial and total. Bibliography.

THE function of the eye, as the peripheral organ of vision, depends on the Retina, *i.e.* that portion of the inner coat of the eye-ball which is formed by the terminal expansion of the optic nerve. Light is its adequate stimulus. Very weak luminous stimuli, as those that come from the stars, suffice to excite the retina, whereas the strongest rays of the sun are ineffective as light-stimuli when they act directly upon cells and nerve-fibres in general. It is accordingly necessary to assume in the end-organ of the optic nerve the presence of a special apparatus (comparable to some extent with a sensitive photographic plate) containing photochemical substances which are capable of liberating potential energy, and thus of producing more effect than the ether-vibrations that act as stimulus.

The first problem in discussing the physiological functions of the retina is to ascertain which of the numerous elements of the retinal tissue are sensitive to light and capable, in consequence of the luminous vibrations of the ether, of liberating the energy required to throw the complex neural apparatus of vision into activity. At the outset, therefore, we have to study the histology of the retina.

I. On examining vertical sections of the human retina and that of the higher animals under the microscope, eight distinct layers at least can be distinguished. Taken from without, inwards, these are :—

1. The layer of pigment epithelium-cells ;

2. The layer of rods and cones (Jacob's mosaic membrane) ;

3. The outer nuclear or granular layer :

4. The outer molecular or reticular layer ;

5. The inner nuclear or granular layer ;

6. The inner molecular or reticular layer ;

7. The layer of ganglion cells :

8. The layer of optic nerve-fibres.

In addition to these, two delicate membranes have been described—the membrana limitans externa between the second and third layers, and the membrana limitans interna between the eighth layer and the hyaloid membrane of the vitreous body.

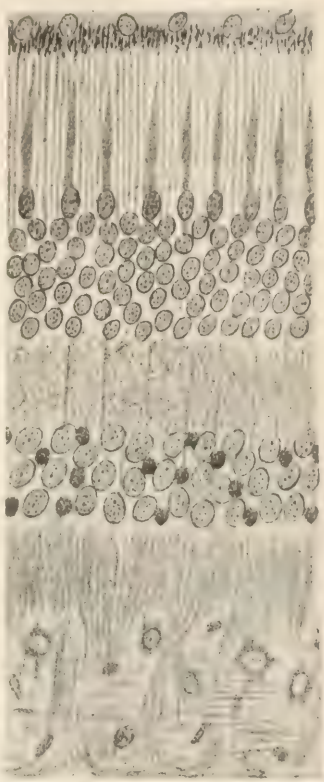


FIG. 154.—Vertical section of human retina, fixed immediately after enucleation of eyeball in Tellyesnieszky fluid. Magnified 510 diameters. (P. Chiarini.) 1, layer of pigmented epithelial cells ; 2, layer of rods and cones ; 3, outer nuclear (granular) layer ; 4, outer molecular layer ; 5, inner nuclear (granular) layer ; 6, inner molecular layer ; 7, layer of ganglion cells ; 8, layer of optic nerve-fibres ; *l.e.*, membrana limitans externa ; *l.i.*, membrana limitans interna.

Fig. 154 shows under a high magnification the appearance of the strata in the retina of a human eye, enucleated from a living man, and immediately placed in a fixing solution.

It is very difficult from this simple figure to form a clear idea of the histological elements of which the retina is built up and of their reciprocal relations. But they have been fully studied by Golgi's silver method and by Ehrlich's vital methylene blue method.

The most external layer (formerly described with the choroid coat) consists of a single stratum of hexagonal epithelial cells, which as seen from the surface form a regular mosaic, and from the side present an outer, nucleated, non-pigmented part, and an inner, pigmented portion prolonged into filiform processes or

fringes, which penetrate between the outer segments of the rods and cones (Fig. 155).

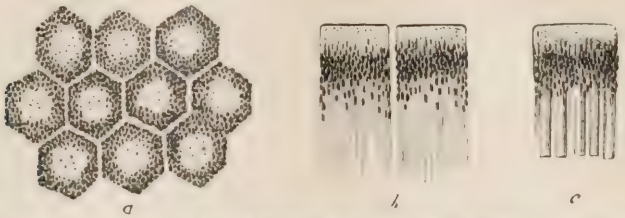


FIG. 155.—Pigmented epithelium of human retina. Highly magnified. (Max Schultze.) *a*, cells seen from outer surface, with clear lines of intercellular substance between; *b*, two cells in profile, with fine processes extending inwards; *c*, cells still in relation with the outer ends of the rods.

The latter are the visual cells, *i.e.* the receptors of the luminous stimuli. In both cones and rods a thinner outer segment can be distinguished from a thicker inner limb: the differences in form, length, and structure are clearly shown in Fig. 156.

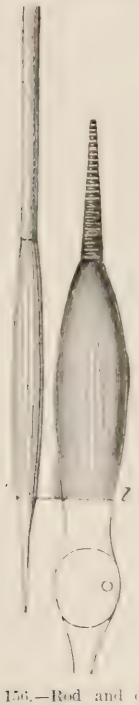


FIG. 156.—Rod and cone of human retina. Highly magnified. (Max Schultze.) Shows the longitudinal striation of both segments of the rod; the cone is transversely striated in the outer, and longitudinally marked in the inner segment; *l*, membrana limitans externa.

The outer segment of both rods and cones consists of a shining, doubly refractive substance, which splits up with certain reagents into a series of transverse discs. The outer segments stain only with osmic acid, and become greenish brown; the inner, on the contrary, can be stained with carmine, iodine, and other dyes.

The rods are more numerous than the cones, except in the macula lutea, which consists exclusively of cones. In the immediate neighbourhood of the macula lutea each cone is surrounded by a single row of rods; in the peripheral portions, on the contrary, each cone is surrounded by several rows of rods; so that the cones become proportionately less frequent with the distance from the macula lutea (Fig. 157).

Both rods and cones are prolonged internally, through the membrana limitans externa into the outer nuclear layer, as fine varicose fibres in which lie their nuclei. The chromatic substance of the nuclei of the rods, unlike those of the cones, has a stratified arrangement (Fig. 158).

The fibres of the rods terminate in small rounded swellings in the outer molecular layer. The cone-fibres also terminate in this layer, as conical dilatations from which short fibres are given off.

The principal elements of the inner nuclear layer are small bipolar nerve-cells, owing to which this layer has also been termed the ganglion retinae. Some of these cells by their arborescences bring the terminations of the rods into connection with the ganglion cells of the seventh layer: others come into contact with the ends of the cone-fibres in the outer molecular layer, and with the protoplasmic processes of the ganglion cells of the seventh layer, by means of their processes, which penetrate the inner molecular layer to different depths.

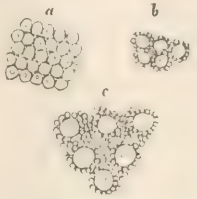


Fig. 157.—Outer surface of layer of rods and cones. 350 diameters. (Kölliker.) *a*, part of macula lutea, where there are only cones; *b*, part near the macula, with only one row of rods between the cones; *c*, part of the retina midway between the macula and the ora serrata, where rods preponderate.

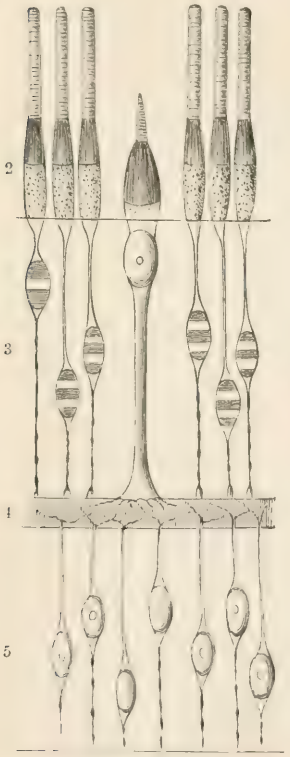


Fig. 158.—Diagram to show some of the neuro-epithelial elements of the retina. (From Schwalbe, modified.) Numbered as in Fig. 154.

Fig. 159 is a diagrammatic reconstruction of the retina. In addition to the elements of the rods and cones, the bipolar cells and the optic ganglion cells (which form a chain of neurones), certain others can be seen, the morphological nature and the real function of which are not exactly known.

At the limit of the outer molecular layer are the so-called "horizontal cells" of Ramon y Cajal, which vary in form and size, and are apparently intended to bring a number of different rods into association.

At the outer limit of the inner nuclear layer there are other cells which send all their processes into the inner molecular layer (spongioblasts, W. Müller; parareticular cells, Kallius). In some of these cells no axis cylinder can be demonstrated (amacrine cells, Cajal). Along with these there are in some animals cells with long processes, which pass directly into the eighth layer, and run with the fibres of the optic nerve.

The optic nerve-fibres, which compose the eighth layer, lose their medullated sheath on entering the papilla (Bowmann), and spread as naked axons in all directions over the retina. The depth of this layer therefore diminishes regularly from the papilla to the ora serrata. Most of the fibres represent the nerve processes of the ganglion cells of the

seventh layer; these accordingly conduct in a centripetal direction, and end by ramifying in the grey matter of the superior corpora quadrigemina and the lateral geniculate bodies. But, according to Cajal, a small number of them are protoplasmic processes of ganglion cells situated in the brain, and are therefore fibres with centrifugal conduction.

The two limiting membranes, outer and inner, are probably formed by Müller's sustentacular fibres, the most important of the elements that bind the structures of the retina together. They resemble the ependymal cells of the embryonic spinal cord. They

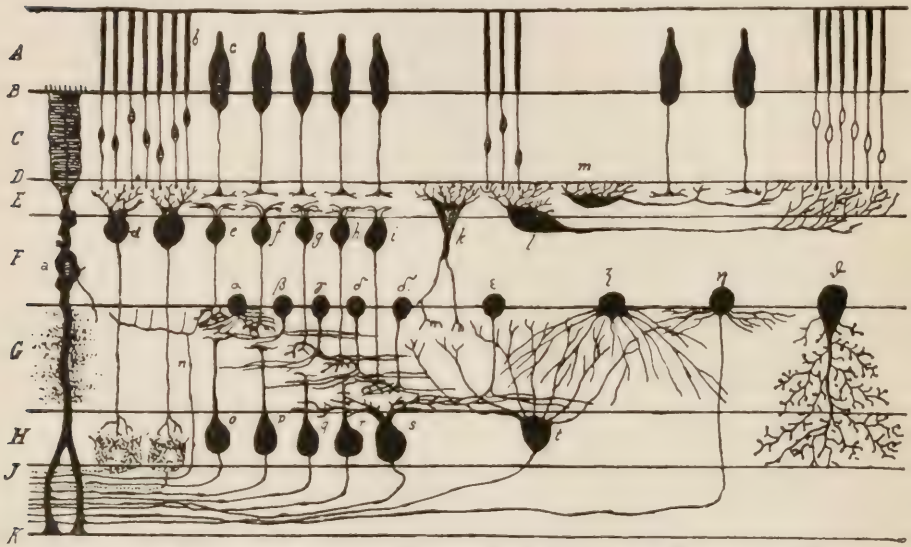


FIG. 159.—Diagram of histological structure of retina, reconstructed by Kallius from Ramon y Cajal. *A*, layer of rods and cones; *B*, membrana limitans externa; *C*, outer nuclear layer; *D*, fibrous layer of Henle; *E*, outer molecular layer; *F*, inner nuclear layer; *G*, inner molecular layer; *H*, ganglion-cell layer; *J*, nerve-fibre layer; *K*, membrana limitans interna; *a*, Müller's supporting fibres; *b*, rods; *c*, cones; *d*, bipolar cell arborising with rods; *e*, *f*, *g*, *h*, *i*, bipolar cells arborising with cones; *k*, *l*, *m*, horizontal cells; *n*, centrifugal nerve-fibre; *o*, *p*, *q*, *r*, *s*, *t*, ganglion cells of optic nerve; *α*, *β*, *γ*, *δ*, *δ'*, *ε*, stratified spongioblasts (amacrine cells); *ζ*, *ϑ*, diffuse amacrine cells; *η*, neuro-spongioblasts.

are epithelial elements of ectodermal origin, small and elongated in form, and scattered through the entire depth of the retina. Their characteristic form is shown at *a* of Fig. 159, and more clearly in Fig. 160.

In addition to Müller's fibres neuroglia cells (spider cells), which occur plentifully along the course of the optic nerve, form part of the supporting tissue of the retina.

This brief sketch of the complicated structure of the retina shows that an excitation produced at the ends of the rods and cones by light must pass through three different ganglion cells (or chain of neurones) before it can reach the brain. The associa-

tion of the three neurones takes place in the two molecular layers by simple contact, or by anastomosis between the terminal arborisations of the axons and the dendrites. In the outer molecular layer the rods and cones come into connection with the internal granules; in the inner molecular layer there is a series of synapses, by which the elements of the internal granules are brought into intimate connection with the cells of the ganglion layer (Fig. 159).

From the physiological standpoint it is important to consider the structural peculiarities of the retina at the fovea and the macula lutea. We have already noted the absence of rods in the fovea centralis where only cones are present, and it must be added that the cones are much longer and narrower than elsewhere. All the other layers of the retina are much thinned, so that the cones are practically in contact with the membrana limitans interna. Towards the edge of the fovea the layers increase rapidly in thickness, and in the rest of the macula lutea they are thicker than at any other point of the retina. Within the fovea the cone-fibres are disposed obliquely, and come into relation with the elements of the inner granules (Fig. 161).

Investigations made by Salzer (1880), in Brücke's laboratory, show that there is not a corresponding fibre of the optic nerve to each cone, the number of cones being three times in excess of the number of optic fibres. While the optic nerve contains about a million fibres, the retina possesses about three million cones, exclusive of the rods—which are 6-7 times more plentiful. Salzer reckoned that there are 13,200-13,800 to every sq. mm. of surface in the fovea.

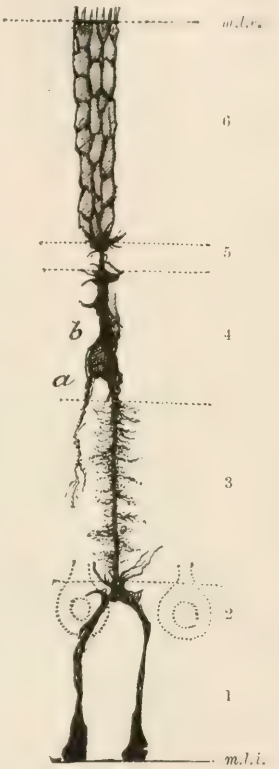


FIG. 160.—A fibre of Muller from the dog's retina, shown by Golgi's method. Highly magnified. (R. y Cajal.) 1, nerve-fibre layer; 2, ganglion-cell layer; 3, inner molecular layer; 4, inner nuclear layer; 5, outer molecular layer; 6, outer nuclear layer; *m.l.e.*, membrana limitans externa; *m.l.i.*, membrana limitans interna; *b*, nucleus of the fibre; *a*, process extending from nucleated part into inner molecular layer.

The fact that not every cone has a separate path to the cerebrum makes it difficult to account for the clear perception of the visual images; but it must not be forgotten that the diameter of the cones does not exceed 2·6 μ, and that those of the fovea are the thinnest (2-2·5 μ according to M. Schultze).

It is also interesting to note that according to Ramon y Cajal

the relations between the cones and the optic fibres in the central fovea have a peculiarity which distinguishes them from those of the other parts of the retina. In the fovea only one cone or two at most (Cajal's *external neurone*) articulate with one element of the nuclear layer (*middle neurone*), and only one or at most two elements of the nuclear layer articulate with one ganglion cell (*internal neurone*). So that in the fovea the paths which conduct the light impulses to the brain are least reduced and least concentrated. From the fovea towards the periphery of the

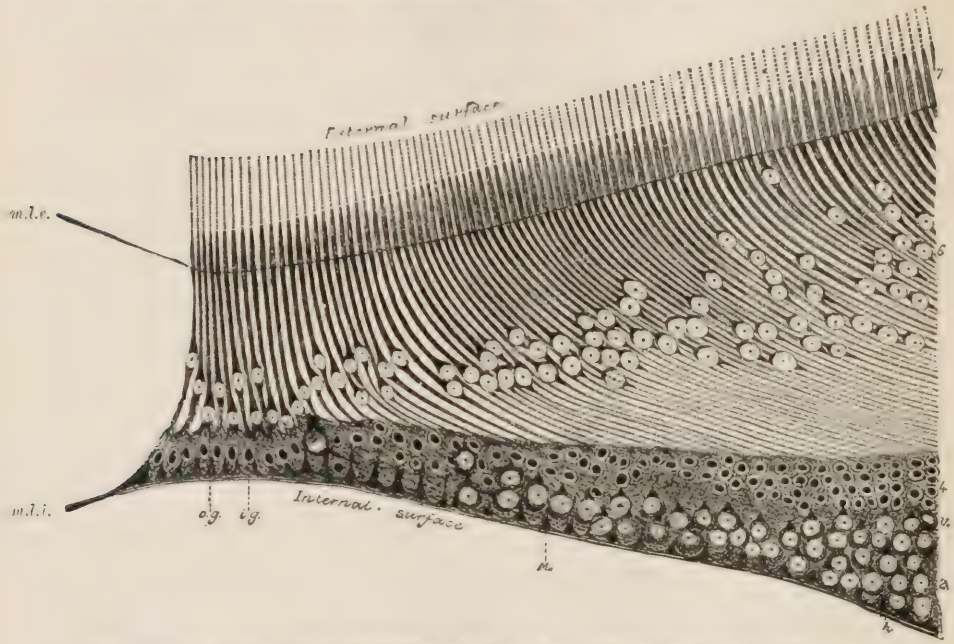


FIG. 161.—Diagram of a section through the fovea centralis. Outlines traced from a photograph. Magnified 350 diameters. (From a preparation by G. N. Golding-Bird.) 2, ganglionic layer; 4, inner nuclear; 6, outer nuclear layer; the cone-fibres forming the so-called external fibrous layer; 7, cones; *m.l.e.*, membrana limitans externa; *m.l.i.*, membrana limitans interna.

macula, on the contrary, and thence towards the outer parts of the retina, the conducting paths are greatly reduced, and the excitations are carried to the brain from an increasing number of rods and cones by a single fibre of the optic nerve.

II. One of the fundamental principles of physiological optics is the fact that when we desire to see an object distinctly we direct our eye towards it in such a way that its image falls on the fovea centralis of the retina. The fovea, which, according to Fritsch, measures 1-1·5 mm. across, therefore corresponds to the area of most distinct vision; it subtends an angle of 3·5-7° with the geometrical axis of the eye-ball or optic axis, which is known as

the visual angle. The perception of objects of which the images fall on the fovea is called *direct vision*, in contrast to *indirect vision* from the peripheral parts of the retina.

Indirect vision is less distinct, and we are unable by it to recognise the outlines, forms, and minute details of objects, but it enables us to distinguish changes and movements within the field of vision, and guides and orientates us, so that we can avoid obstacles

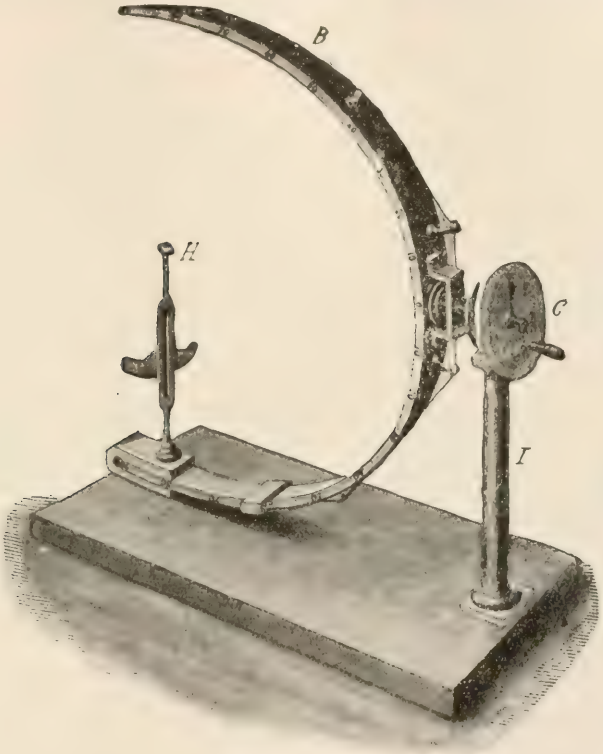


FIG. 162.—Förster's perimeter.

in walking (S. Exner). It becomes increasingly less acute and more blurred in proportion as the images fall on the retina farther from the fovea and nearer the periphery.

The visual field does not coincide with the whole area of the retinal surface. Its extension varies in different individuals, in different meridians, and even to a slight extent in the two eyes, under both normal and abnormal conditions. The field for white is most extensive, and next in order come those for blue, red, and green.

The perimeter is used to determine the range of indirect vision.

By its means a small white or coloured object can be presented to the subject in any meridian of the field and at any distance from the fixation point.

Forster's perimeter (Fig. 162), on which all others have been modelled, consists of a half-circle *B* of metal, marked with a scale. A runner to which small white or coloured discs can be fastened moves along its blackened concave surface. The middle of the arc, which is fixed in a horizontal axis around which it can rotate, forms the point of fixation. An indicator *C* shows the position of the meridian examined on the opposite side of the axis.

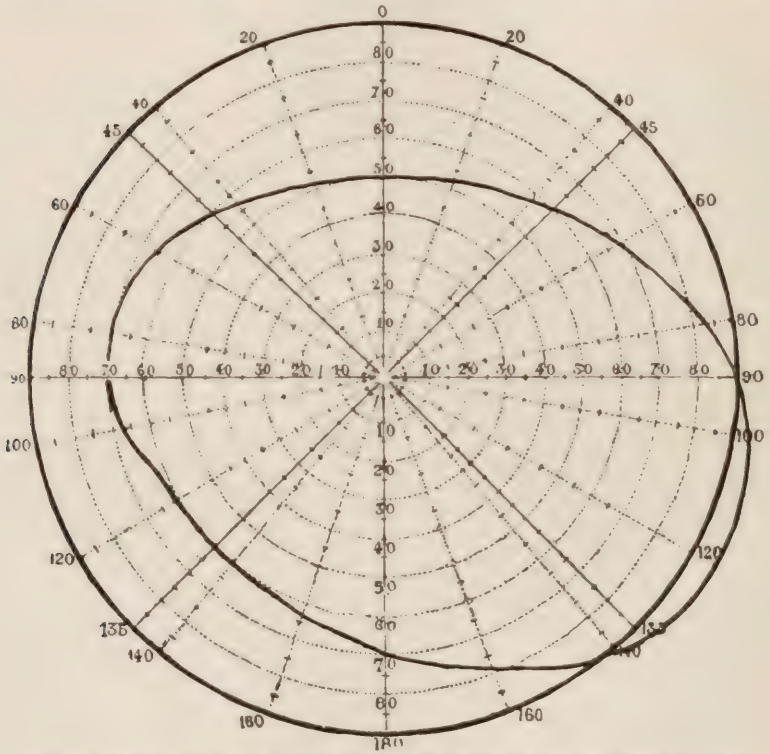


FIG. 163.—Normal visual field of right eye of an individual aged 40, with a *white* square of 20 sq. mm. (Luciani.)

The subject rests his chin on a support H. The perimeter is graded so that the zero point is in the centre.

The subject is so placed that the eye to be examined is at the level of the centre of the perimeter, and he is asked to look at the fixation point, the other eye being blindfolded to avoid confusion. The runner with the disc is then moved slowly from the periphery to the centre, and the subject is asked to indicate the moment at which he first sees it, while his eye remains fixed on the centre of the arc. The corresponding degree is then read on the convex surface of the arc, and the position of the meridian is also noted. When this operation is repeated in different meridians the field of vision can be represented graphically on a chart (Fig. 163). The zero *O* corresponding to the

point of fixation is at the centre of the chart; the concentric circles 10° apart correspond to the perimeter scale; the meridians are drawn at each 20°.

On comparing a number of visual fields mapped out carefully from normal eyes there are found to be differences which may amount to 15° or more in certain meridians. It is therefore impossible absolutely to define "a normal field of vision." Landolt gives the following figures for white:

Above	70°
Above and outward	60°
Outwards	90°
Below and outward	85°
Below	60°
Below and inward	55°
Inwards	55°
Above and inward	55°

In making observations by means of the stars G. Ovio (1903) found the extent of the visual field to be far wider than is usually



FIG. 164.—Method to demonstrate Mariotte's *blind spot*.

supposed—about 90° in all directions, and even beyond 90° on the temporal side.

The more the object is illuminated the farther can it be seen on the periphery; large stars are therefore seen farther from the fixation point than small stars.

Another fundamental fact was discovered by Mariotte (1668). He found in the region of the visual field which corresponds to the position of the papilla of the optic nerve an area that is completely insensitive to light, and is therefore known as the *blind spot*.

To demonstrate its presence on one's self, it is only necessary to close the left eye, and fixate the white cross of Fig. 164 with the right, at a distance of 25-30 cm. On moving the book a little nearer to or farther from the eye it is easy to find the exact distance at which the white disc to the right is totally invisible, so that the black ground appears continuous. A black disc on a white ground may be employed instead of a white disc on a black

ground; the black disc then disappears and the background appears entirely white.

The blind spot is so large that at a distance of 1·7-2 m. the head of an adult man may be invisible. Helmholtz succeeded in obtaining an exact measurement of the blind spot in his right eye by looking fixedly at a point on a white surface, and then moving the blunt end of a pencil to and fro within the blind area. By drawing on the paper the points at which he began to see the end of the pencil and joining these points by a continuous line, he obtained Fig. 165, in which *a* represents the point fixated, *d* the shape of the blind spot, the line *AB* the third part of the distance between point *a* and the observer's eye. As the figure shows, the blind spot corresponds exactly with the shape of the papilla of the optic nerve and the main trunks of the central arteries issuing from it. Donders also demonstrated the insensibility of the papilla to light. When the image of a flame is thrown on to the optic papilla by an ophthalmoscope, the subject does not perceive it, although a slight inclination of the mirror makes the image perceptible.



FIG. 165.—Form of Mariotte's blind spot. (After Helmholtz.)

It is thus evident that the nerve-fibres of the optic papilla are totally inexcitable to light, and that the cones are the specific receptor apparatus of luminous stimuli for direct and distinct vision. We know that the cones become gradually less, and the rods between them more numerous, towards the outer parts of the retina. Indirect and blurred vision in the periphery of the visual field may be explained on the assumption that cones and rods alike are excitable to light, but that cones alone are capable of arousing visual sensations, the sole function of the rods being to excite unconscious reflexes. This hypothesis proposed by Gad (1894) is, however, disproved by the fact that only rods are present in the retina of rabbits and other rodents, cones being entirely absent even from the fovea. Again, we know from the work of Cajal and Retzius that rods as well as cones are in connection with the external bipolar cells (second neurone) and with the ganglion cells (third neurone), even if the conducting paths are more reduced and concentrated than in the cones (Fig. 159).

The "duplicity theory," first formulated by M. Schultze (1886) and confirmed by the subsequent work of Parinaud and v. Kries, assumes that the rods as well as the cones are organs of visual

perception, although they differ fundamentally both in function and in structure.

III. The retina presents marked alterations according as it is exposed to light or darkness. These changes, which represent the reaction of its elements to the luminous stimuli, are sometimes visible macroscopically, sometimes only under the microscope: some are essentially chemical in character, others physical and anatomical.

The analytical study of these objective changes due to stimulation of the retina is of great interest. It forms the starting-point of a new chapter, evolved entirely out of recent researches, and directed to the establishment of a rational theory of vision—more exactly of a physiological theory to explain the physico-chemical process by which the luminous vibrations can produce that excitation of the rods and cones which is necessary to evoke sensations of light and colour in the cerebral centres.

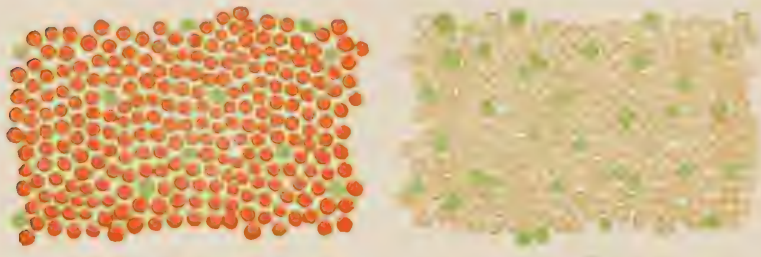
Heinrich Müller (1851) was the first who observed that the rods of the frog's retina are sometimes coloured red. Leydig (1857) stated that a red colour is present in the rods of all amphibia; M. Schultze found that those of the mouse and owl were also red. But the discovery of the colouring matter of the rods in the retina of most vertebrates, and of its transformation under the influence of light, was made by Boll, who gave it the name of *retinal* or *visual purple.*

In his memorable paper "On the Anatomy and Physiology of the Retina," presented to the Accademia dei Lincei, December 3, 1876, he clearly demonstrated that the outer segments of the rods secrete a red substance which gradually discolours under the influence of light. When the retina of a frog or rabbit that has been kept for several hours in the dark is examined in the fresh state it looks red, but bleaches fairly rapidly under white or monochromatic light. Decoloration sets in after 5 and is complete at the end of 15 minutes. According to Boll, the visual purple regenerates as fast as it is consumed, but only accumulates in darkness, and reaches its maximum in two hours. Its regeneration appears to be connected with the presence of the pigment epithelium which covers the external surface of the retina; this may provide the material for the formation of the purple. In the frog's retina, in addition to the rods that contain the purple, Boll detected others, scattered here and there, which are pale green in colour (Fig. 166). He also first described how the pigment from the epithelial cells wanders down between the interstices of the rods and cones under the influence of white and monochromatic light, and he recognised the great importance of this fact in the theory of vision. "The physiological elements," he writes, "which perceive light and colour are highly complex anatomical structures; they must include the rods and cones on

the one hand and the cells of the pigment epithelium on the other. As in the organs—muscles, electrical and luminous organs—provided with centrifugal nerves, so, too, in the sense-organs provided with centripetal nerves definite material alterations of a physical, chemical, and anatomical character correspond to the physiological states of rest and activity."

Kühne (1877–79) successfully continued and developed Boll's researches on visual purple, but unjustifiably attempted to claim the credit of its discovery. He proved that it was not an interference colour, but a true pigment, as Boll had also stated: that it is soluble in a solution of bile acids or their salts; and that, consequently, the changes which the visual purple undergoes in white or coloured light come under the category of photochemical phenomena.

According to Kühne, visual purple resists the death of the tissue, putrefaction, and desiccation, so long as it is protected from



A B

FIG. 166.—To show mosaic of rods in frog's retina. (Boll.)
A, after prolonged exposure in darkness; B, after longer exposure in violet light.

the action of light. It also resists a number of oxidising and reducing chemical reagents; but it is destroyed by most acids and caustic alkalies, by alcohol, ether, chloroform, etc.

Visual purple can be fixed by 4 per cent solution of alum, and preserved for a certain time from the decomposing action of light, although it becomes more or less altered. By this means Kühne succeeded in obtaining *optograms* or photographic images on the retina of rabbits or frogs, similar to those on photographic plates. For this purpose the animal, which had previously been atropinised and kept in the dark, was placed for 1½ minutes in front of a window, and then killed; the retina was dissected out in yellow sodium light, and the image fixed by the alum solution. Even after several days the image of the window, etc. could be plainly seen. As shown in Fig. 167, the illuminated part of the window was white, and the remainder pink.

Kühne further confirmed and demonstrated the fact already pointed out by Boll that the origin of retinal purple in the outer part of the rods is associated with the pigment epithelium.

He found that a retina, previously dissected and bleached by light, can recover its red hue if it is again brought into contact with pigmented epithelium in the dark. This influence of the epithelium cannot, however, depend on the *pigment*, because the regeneration of visual purple takes place also in the retina of albino rabbits, in which the epithelium contains no pigment.

Researches subsequent to the work of Boll and Kühne have added little to our knowledge of the rhodopsin (erythropsin) or visual purple. It is now proved to exist in all classes of animals in which the retina is provided with rods—except pigeons and fowls—and to be absent in retinae that contain only cones. Schenck and Zuckerkandl found rhodopsin in the retina of an executed criminal; Fuchs and Velponer found it also in the retina of the human foetus of 7-9 months.

Previous to the discovery of visual purple, Helmholtz (1855) and Setschenow (1877) had noted that the retina observed under ultra-violet light is fluorescent. Kühne pointed out that this fluorescence cannot be due to the rhodopsin, because retinae previously exposed to bright light and thus entirely colourless and transparent are more fluorescent than those previously kept in the dark and charged with purple. Obviously the fluorescence must depend on the colourless derivatives of the rhodopsin. Nagel and Himstedt (1902) found that colourless solutions of visual purple in sodium glycocholate are more fluorescent than simple solutions of bile salts. On the other hand, the retina of pigeons is also fluorescent, particularly after exposure for a few minutes to daylight, although it is entirely destitute of purple.



Fig. 167.—Optogram or photograph on retina obtained by Kühne.

The pigmented epithelial layer of the outer surface of the retina prevents ophthalmoscopic observation of the visual purple in man and in most living animals (Becker, Coccius). In fishes, on the contrary, which have a white tapetum behind the layer of rods, *e.g. Abramis brama*, it can be seen and its discoloration watched by means of the ophthalmoscope (Abelsdorff).

Immediately after the discovery of the visual purple not a few hoped with Boll that it might represent an important factor in the construction of a complete physiological theory of vision. But we are now forced to admit that vision is entirely independent of the retinal purple. There is none in the cones, and therefore in the fovea—where vision is most acute; in pigeons and fowls the rods are destitute of purple; snakes have only unpigmented cones. Kühne made investigations to determine if in the rabbit's retina, in which only rods are present, the purple is the substance which on its decomposition excites vision; but he was forced to

conclude that rabbits, too, can see perfectly after the purple has been broken up by sunlight, before it can be regenerated. There is no doubt that the accumulation of rhodopsin in the rods coincides with an enormous increase in their sensibility to light; but we do not know if this really depends on an accumulation of the purple, or on other concomitant chemical changes that take place in the dark. The discovery of a highly photo-aesthetic substance in the retina nevertheless makes it very probable that in all the elements of the retinal mosaic other photo-aesthetic substances may exist which have not yet been detected, owing to their being colourless, but which, by the alterations induced in them by the luminous vibrations of the ether, may be capable of exciting the peripheral and central neural apparatus of vision.

Of no less interest are the anatomical alterations, or better the phenomena of movement, observed in the retina under the influence of light and darkness.

We have said that Boll first described in the frog the movement of the pigment granules of the retinal epithelium along the filiform processes that penetrate between the rods and cones (1876). Angelucci (1878), continuing Boll's work on the frog, was able better to observe this displacement of pigment, and found that in darkness it travelled as far as the upper third of the outer segments of the rods, while under the influence of light it ascended to the membrana limitans externa. He further saw that the movement of the pigment granules coincides with a contraction of the protoplasm of the pigmented epithelial cells. Under the action of light, both the outer unpigmented part and the pigmented base of these latter diminish in height, while in the dark both parts thicken considerably. Finally, he noted that both the displacement of the pigment granules and the contraction of the retinal epithelium increase progressively under monochromatic light from red to violet, that is from the less to the more refractive rays.

Kühne (1879) observed in the frog that the retinal pigment (fuscin) disappears under the protracted action of light. This fact was fully confirmed in fishes by Pergens (1896) and Chiarini (1904), who further noted that after the fuscin had been entirely used up by prolonged action of direct sunlight it was slowly regenerated in the dark, and only attained its maximum after 15-20 hours (Fig. 168).

Angelucci (1882) also found that the rods contracted under the action of white and monochromatic light; but he failed to detect the striking fact that the inner segments of the cones contract, which was discovered by van Genderen-Stort (1884). This observation, which has been confirmed by all later workers, completes the series of important morphological changes in the

retina due to the protoplasmic movements observed under the action of light.

The contraction of the outer limbs of the rods, described by Angelucci (1884) and his pupils, and the contraction of the inner segments, as observed by Gradenigo (1885), were subsequently disputed by van Genderen-Stort, by Greeff, and by Chiarini from exact measurement and comparison. According to van Genderen-

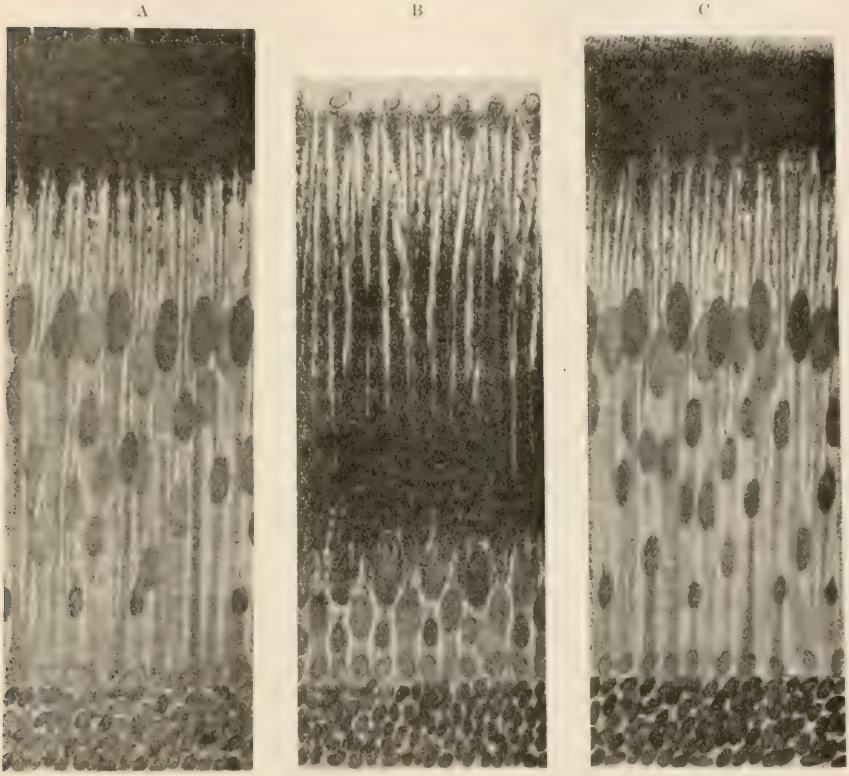


FIG. 168.—Vertical section of temporal half of retina of *Lacerta viridis*, fixed in Flemming's fluid. (P. Chiarini.) A, after keeping the animal 24 hours in the dark; B, after exposing it for 6 hours in direct sunlight; C, after exposing it for 5 hours in direct sunlight, and subsequently for 1 hour in total darkness.

Stort, Greeff, and Chiarini, when a frog is exposed to light the inner limbs of the rods merely suffer a passive change of form, due to pressure from the ellipsoidal bodies of the cones which approach the external limiting membrane (Fig. 169).

Another important fact was discovered by Engelmann (1885), who found that the movements of the cones and pigment-cells of the retina under light are directly dependent on the nervous system. He saw that when one eye only of the frog was exposed

to light the pigment descended and the cones contracted, even in the eye that remained in the dark. He further noted that the same effect could be produced in both eyes on exposing the back and the hind-limbs of the frog to light, while the eyes were kept in darkness. This reflex action of the nervous system does not occur with the visual purple—which only changes in the eye that is directly illuminated, and undergoes no appreciable alteration in the retina that is kept in the dark.

The reflex action on the cones and pigment-cells of the retina may also be seen in decapitated and bloodless frogs, provided the

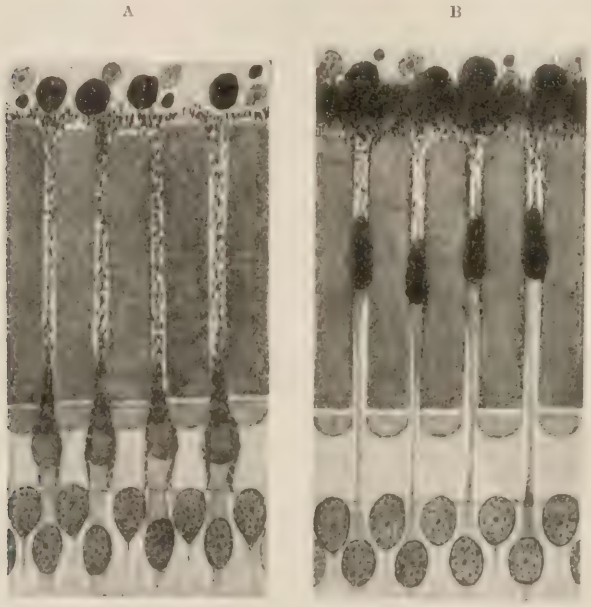


FIG. 169.—Vertical section of temporal half of retina of *Rana esculenta*, fixed in Flemming's fluid. (P. Chiarini.) A, after keeping the animal in direct sunlight for 6 hours; B, after keeping it in the dark for 24 hours.

brain is left intact; once the brain is destroyed, the light only affects the illuminated eye. To explain the transmission of excitation from the retina or from the skin to the brain, and thence to the "myoid" elements of the retina, Engelmann assumed the presence in the optic nerve of centrifugal or retino-motor conducting paths—which, as we have seen, were directly demonstrated by Cajal (Fig. 159).

Fick disputed Engelmann's conclusions, but they were confirmed by Nahmacher (1893), who observed movement of the pigment and contraction of the cones in frogs kept in darkness, on stimulating either the chiasma or the optic nerve with sodium

chloride. If one of the optic nerves had been cut, the consensual reflex reaction did not appear.

Fresh confirmation of Engelmann's experiments was adduced by Lodato and Pirrone (1900) and, by an ingenious modification, by Chiarini (1904).

These morphological changes in the retina, which result from the action of light and darkness, are mostly developed in fishes and amphibia (Figs. 168, 169): they can be seen, but to a less extent, in the retina of reptiles and birds (Figs. 170-171), and are scarcely appreciable in mammals and man. This is proved by the researches of Angelucci, of van Genderen-Stort, and, more recently, of Chiarini and Garten.

Lizards exhibit all the changes described in *Leuciscus* and in the frog, especially the movement of pigment and shortening of the contractile part of the cones, which alone form the mosaic layer, as these reptiles have no rods (Fig. 170).

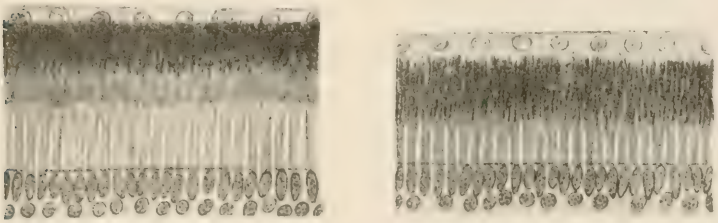


FIG. 170.—Vertical section of temporal half of retina of *Lacerta agilis*, fixed in v. Tellyesnieszky's fluid. Magnified 510 diameters. (P. Chiarini.) A, after keeping the animal in the dark for 24 hours; B, after exposing it to direct sunlight for 6 hours.

In ravens the migration of pigment is even more marked than in lizards, and with prolonged action of sunlight it entirely leaves the body of the cell and wanders into the filiform processes. The layer of retinal cells consists in birds of long, fine rods and cones of varying thickness, which contract on exposure to sunlight in the inner segments only (Fig. 171).

It is far more difficult to study the slight morphological changes in the mammalian retina. Guinea-pigs and rabbits are of little use for such experiments because their retina contains no cones: in dogs the cones are very few and extremely slender; in pigs and monkeys they are more numerous and well-developed. Van Genderen-Stort first demonstrated shortening of the cones under the action of light in the pig; Chiarini failed to detect any difference in light or darkness in the few slender cones of the dog. Garten's experiments on monkeys (*Macacus* and *Cercopithecus*) led to very doubtful results, because the differences of length (measured between the membrana limitans externa and the ellipsoidal base of the cones) in retinae exposed to light, and those

kept in darkness, are so small (0·1-0·2 m.) that they may be reckoned as errors due to fixation.

Equally doubtful are the observations on the displacement of pigment in mammals generally. Angelucci (1878) found that in rabbits—including albinos—exposed to light it was difficult to dissect away the epithelial layer from the underlying layer of the rods after the eye had been fixed in osmic acid, without tearing the outer portion of the rods; this did not occur when the eye had been kept in the dark. In dogs, also, Chiarini observed this greater cohesion between the retinal epithelium and the rods and cones in animals exposed to sunlight. This fact does not depend on the wandering of pigment, because it also occurs when the epithelium contains more. So that structural changes due to light are not merely inconspicuous in the retinal elements

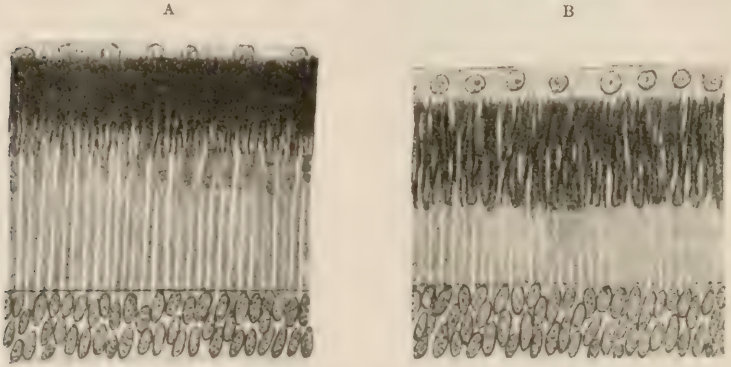


FIG. 171.—Vertical section of temporal half of retina of *Cercus cornix*, fixed in v. Tellyesnieszky's fluid, magnified 510 diameters. (P. Chiarini.) A, after keeping the animal in the dark for 24 hours; B, after exposing it to direct sunlight for 6 hours.

of mammals, as Angelucci stated, but are, as Chiarini says, rudimentary.

The fact that in the higher animals, in which vision is most developed and differentiated, the movement of the fuscin and contraction of the cones either do not occur, or are rudimentary, prevents the inclusion of these phenomena as essential factors in a general theory of vision. But this does not preclude us from studying the nature and functional value of the objective changes with which vision is associated in the lower animals.

The wandering of fuscin from the epithelial cells into the protoplasmic processes between the rods and cones upon exposure to light cannot be considered as a passive displacement due to the contraction of these cells—as assumed by Angelucci. If this were true, the body of the epithelial cell could never remain completely destitute of pigment, as is the case after prolonged exposure to direct sunlight. Nor is it more accurate to regard it

with Kühne as a heliotactic or phototactic phenomenon, because, as we have seen, it may be induced reflexly, and not by light alone, but by other physical and chemical stimuli. Chiarini's hypothesis seems more acceptable. He regards the migration of the pigment and the greater cohesion between the retinal epithelium and the layer of rods and cones in animals influenced by sunlight, as a chemotactic phenomenon, by which the rods and cones are provided with the materials necessary to make good the loss suffered during their functional activity. This view, supported also by Pergens and others, agrees with the observations of Boll and Kühne that the retinal epithelium is indispensable to the regeneration of the purple, although the latter is—at least to some extent—independent of the fuscin, since it exists in albino rabbits, in which the epithelium is altogether destitute of pigment.

In addition to the nutritive function, Angelucci assigned to the migration of the fuscin the office of protecting the sensitive elements of the retina from unduly intense light, and of counteracting the effect of dazzle in the eyes of albinos which have no pigment. But this protective function is common to the pigment of the choroid and iris as well as to the fuscin, and must be independent of its movement. And, on the other hand, we have seen that the protective rôle of fuscin can only be rudimentary in mammals and in man, where the retinal pigment is very scanty, so that the rods and cones are almost entirely exposed (Fig. 154).

The retinal epithelium undoubtedly plays a certain part in the adaptation of the eye to intense light and twilight. "When the retina is affected by strong light it functions with greater activity; its nutritive exchanges are more active and its consumption greater; and to provide for this increased consumption the connection between the retinal epithelium and the pigment on the one hand, and the layer of rods and cones on the other, is more intimate. When, on the contrary, it is exposed to weak light, or better is kept in complete darkness, its functional activity is diminished or suspended, its nutritive exchanges are less active, its consumption is reduced to the lowest terms, and in consequence the connection between the epithelium and the rods and cones is less intimate" (Chiarini). That is, *positive chemotaxis* in the first case, *negative chemotaxis* in the second.

The *electromotive phenomena* that can be observed in the retina are connected with the contraction of the retinal epithelium and the contracted segments of the cones under the action of light.

As early as 1849 du Bois-Reymond observed that when an entire living eye, or the isolated retina of any vertebrate, was brought into circuit, by means of unpolarisable electrodes with a good galvanometer, a current, which he termed *current of rest*, could be led off. According to Holmgren (1866–71), on joining up the cornea of the frog's eye and the stump of the optic nerve, the

latter is found to be electrically negative to the former, while it is positive to the postero-lateral part of the eyeball. In the isolated frog's retina, again, the periphery is negative to the point at which the optic nerve enters and to the outer surface, but positive to the inner surface of the retina. According to Kühne and Steiner, the outer surface is negative to the inner surface of the retina.

The magnitude of the current of rest differs in different cases; it falls rapidly in preparations from warm-blooded animals, much more slowly in the cold-blooded; in the isolated frog's retina it lasts many hours.

According to Holmgren, the current of rest exhibits a variation when the "dark" retina is suddenly illuminated: or when the previously illuminated retina is darkened. The strength, direction, and course of this *current of action* vary considerably with the kind of animal and form of the preparation. The frog lends itself to these experiments better than any other animal, on account of the long persistence of its current of rest.

The typical reaction in a frog's eye, as little injured as possible, is as follows: Sudden illumination produces after a brief latency a *positive* oscillation of the current of rest, which attains its maximum after a few seconds, and then slowly diminishes if the illumination is continued. A sudden transition to darkness produces another positive variation, the *after-effect*, but this is transient, and is followed by a slow return to the position of rest.

In mammals, birds, and reptiles, even under normal conditions —that is, with the retina intact—illumination gives rise to a negative, darkness to a positive oscillation (Holmgren); to this rule there are, however, exceptions (Nagel and Himstedt.)

These photo-electrical reactions are probably phenomena concomitant with the chemical changes produced by the stimulus of light in the sensitive elements of the retina. But little or nothing is at present known as to their functional significance and specific cause. It is highly probable that the electromotive phenomena originate in the sensitive elements of the retina. They were, in fact, observed by Beck in the retina of Cephalopods (*Eledone moschata*), which consists only of rods and cones, as the elements of the other retinal layers are only found in the optic nerve and ganglion.

IV. Stimulation of the retina produces neural impulses, which on transmission to the brain excite psycho-physical phenomena, *i.e.* physiological processes intimately connected with states of consciousness. These are the *specific visual sensations*, which are sometimes associated with the sensation of "dazzle."

The fundamental differences in the sensations that reach us through the eyes are differences in *brightness* or luminosity and in *colour*: in other words, visual sensations may be *colourless* or *coloured*. The former are distinguished from one another only by

differences of intensity, that is, by different degrees of brightness; the latter present both quantitative and qualitative differences, represented by the different colours.

There are a great number of coloured sensations, each of which may not only present different degrees of brightness, but may also differ from colourless sensation according to their degree of saturation. The greater this difference, the more the colour is said to be *saturated*; the less it is, the *paler* the colour. Thus we may have bright-saturated, or dark-saturated, bright-pale, or dark-pale sensations of colour.

The physiology of the visual sensations consists fundamentally in determining the relations between the varying intensity and quality of the sensations and the quantitative and qualitative differences in the specific stimuli by which they are produced.

We know from physics that the white light given out by the sun consists of a complex of ether vibrations of different wave-lengths, which by means of a prism can be resolved into the so-called *solar spectrum*, owing to the different refrangibility of the rays of which it is composed. These rays do not appear to us white, like sunlight, but coloured. The colours of the spectrum are in the following order—red, orange, yellow, green, blue, indigo, and violet. Red is due to the least refrangible rays; violet to the most refrangible. The intermediate colours are due to rays of which the refrangibility increases gradually in the series from red to violet.

The degree of refrangibility of the different rays depends on their different rate of velocity through solid or fluid media. They further differ in the number of their vibrations and in their wave-lengths. Measured in $\mu\mu$ ($= \cdot 0001\ \mu$), this varies as follows for the different simple colours:—red = 760-647; orange = 647-586; yellow = 586-535; green = 535-492; blue = 492-456; indigo = 456-424; violet = 424-397 (Fig. 172).

There is a continuous series of gradations between the colours of the spectrum, for the expression of which no simple and universal terms exist in language. But the number of colours and hues represented in our spectrum does not include the whole of the colour impressions our eyes are capable of perceiving: there is no shade of *purple*, which is produced by the mixture of red and violet, that is, of the two end-colours of the spectrum.

The solar spectrum is not confined to the portion that our eyes can appreciate. Beyond the red there are rays of greater wave-length than 760 $\mu\mu$ (*ultra-red rays*), and beyond the violet, rays of lesser wave-length than 397 $\mu\mu$ (*ultra-violet rays*). The former are *heat* rays, the presence of which can be detected by means of a thermo-electric couple: the latter are *chemical* or *actinic* rays, the existence of which is revealed by the chemical effects which they produce upon certain salts of silver.

On the other hand, the thermal, photic, and chemical action of

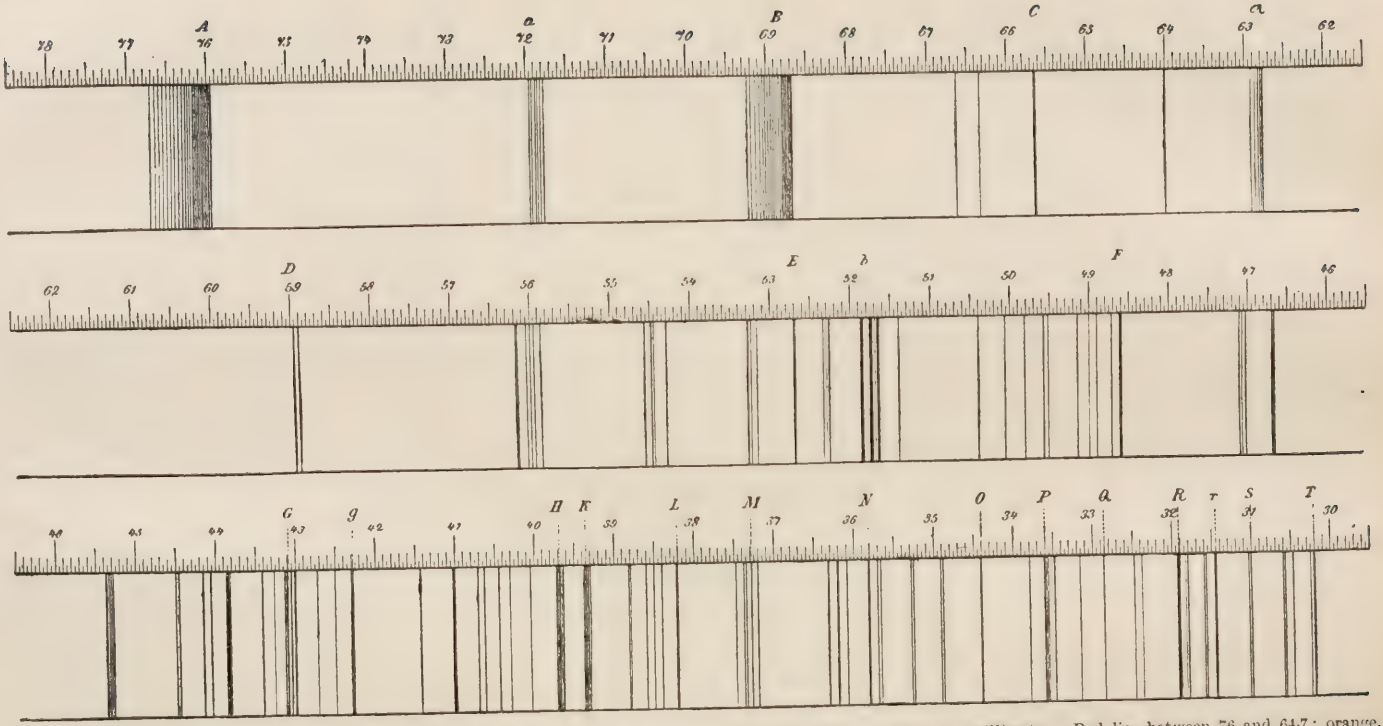


FIG. 172.—The solar spectrum. (After Hasselburg.) The figures indicate the wave-lengths in hundred-thousandths of a millimetre. Red lies between 76 and 64·7; orange, between 64·7 and 58·6; yellow, between 58·6 and 53·5; green, between 53·5 and 49·2; blue, between 49·2 and 45·6; indigo, between 45·6 and 42·4; violet, between 42·4 and 39·7.

the solar radiations is not confined exactly to the three different parts of the spectrum. The photic rays of the less refrangible portion, as red, orange, yellow, are also thermal; the visible rays of the more refrangible portion, as green, blue, indigo, violet, are actinic in proportion to their refrangibility. From this fact we conclude that all the radiations that make up the spectrum as a whole, both visible and invisible, are of the same nature—that is, they consist of ether vibrations which differ only by their differing refrangibility or wave-length.

The visible part of the spectrum, which under ordinary conditions is limited by the extremes of red and violet (line *A* to line *H* in Fraunhofer's spectrum), may under special experimental conditions extend for a certain distance into the ultra-violet region. Helmholtz found that when the ultra-violet part of the spectrum was made to pass through the slit of a diaphragm, and then to fall upon a second prism so as to exclude all the extraneous elements by a new refraction, the eye appreciates a portion of the ultra-violet region, from line *H* to line *R*, Fraunhofer, as a lavender-hued sensation.

The portion of the spectrum which we perceive as coloured consists of rays, the wave-length of which decreases gradually from 760 $\mu\mu$ (line *A*) to 397 $\mu\mu$ (line *H*); the ultra-violet portion of the spectrum, which is faintly visible as lavender when all the rest of the spectrum is cut out, lies between 397 and 320 $\mu\mu$ (line *R*). The whole of the visible portion of the spectrum thus occupies a less interval than a complete octave; the dimly visible part occupies an interval of about a minor sixth. We may therefore conclude that the visibility range of the ether vibrations is much smaller than the audibility range of the vibrations of ponderable bodies.

On what does the invisibility of the radiations of the extreme regions of the spectrum depend? Obviously there are two possibilities: either the rays may be absorbed by the different transparent media of the eye and do not therefore act on the retina—or the ultra-red rays are too slow, and the ultra-violet rays too rapid, to excite its sensitive elements.

Special experiments have been made to measure the absorption of the thermal rays, when they pass through the dioptric mechanism of the eye. The observations made by Aschkinass on the human eye showed that only rays with a wave-length of 872 $\mu\mu$ are absorbed to an amount of 10 per cent, so that the greater part of the ultra-red rays easily pass through the transparent media of the eye without undergoing appreciable absorption. To explain their invisibility we must therefore assume that their vibrations are too slow to excite the receptors of the retina, just as vibrations of unduly prolonged sound fail to excite the receptors in the internal ear.

Different opinions have been held at different times in regard to the penetrability of the ultra-violet rays through the eye. The view put forward by Brücke (1845) is now generally accepted, that they are almost completely absorbed by the transparent media of the eye and by the lens in particular. In fact the researches of Chardonnet, which were confirmed by Gayet and by Widmark, showed that patients who had been operated on for cataract perceived the more refrangible part of the spectrum, which is invisible to the normal eye. So that, unlike the ultra-red rays, the ultra-violet are absorbed by the lens, and after its removal they become visible to a certain extent. According to Widmark, the visibility of the most refrangible end of the spectrum varies for the human eye between rays of 395 $\mu\mu$ and of 371 $\mu\mu$ wave-length, while in the absence of the lens it extends to the rays of 313 $\mu\mu$. According, on the contrary, to Mascart and others the extreme limit of visibility extends to the rays of 210 $\mu\mu$. Beyond this the ether vibrations become so rapid that they no longer excite the receptors of the retina, just as sound-waves that are too short fail to throw the receptors of the cochlea into activity. The Röntgen rays are invisible owing to their excessively short wave-length, but according to Dohrn and others they become visible to a certain extent when very intense.

It follows that ether waves of moderate length alone are capable of exciting the sensory elements of the retina, and that what we call light and colour depend on the intrinsic property of our receptor apparatus to react to certain vibrations only. We can imagine the existence of eyes, sensitive not like ours to the medium, but solely to the extreme vibrations of the ether. Such an eye would view the world under an aspect very different from that in which we see it; the thermal or the chemical radiations would be perceptible in the form of colours never seen by us, and which we are unable to imagine, because they are qualitatively different from those which our vision can appreciate.

All colours found in nature or produced by art can be obtained from the colours of the solar spectrum, although it does not contain the whole of the visible rays, since those corresponding to Fraunhofer's lines are wanting. The mixture of all the spectral colours, in the proportion in which they exist in the spectrum, produces the white light of day. Grey is only white of low intensity; black is the colour of the objects that do not give off or reflect rays capable of exciting the retina.

The different sources of artificial light contain different rays in different proportions. Strontium light, for instance, contains chiefly red rays; sodium light, yellow rays. When these and the other artificial lights are analysed by means of a prism, the spectra obtained are not continuous, but consist of distinct bands,

varying in number, which are characteristic of the different chemical elements.

The colours of the various bodies that do not give out light depend on their capacity for reflecting if they are opaque, or refracting if transparent, certain of the light-rays, and of absorbing all others. Their colours are saturated in proportion to the quantity of rays of any given wave-length which they reflect or refract; brighter, in proportion to the total of visible rays which they reflect and refract—darker, according to the number of visible rays they absorb.

V. In order that the radiations of the ether shall be able to excite the retina, it is essential, not only that their wave-length—on which their visibility depends—shall fall between red and violet of the spectrum, but that two other conditions shall be fulfilled, namely, they must have a certain *intensity* and a certain *duration*.

The intensity of a luminous sensation depends on the amplitude or kinetic energy of the ether vibrations that excite it, and on the degree of retinal excitability at the moment of stimulation.

The threshold stimulation, *i.e.*, the minimum of luminous intensity essential to vision, is usually very low. By a method of great delicacy Aubert found that the normal eye is capable of perceiving light one million times weaker than ordinary daylight. Other conditions being equal the threshold of retinal excitability also varies within physiological limits in different subjects. Astronomers know, in fact, that many people are able to see certain stars which are invisible to others apart from any ametropia of the eye.

The normal eye is capable of distinguishing which is the brighter or stronger and which the duller or weaker of two luminous sensations. The minimal objective difference in intensity of two lights which the eye is capable of recognising is known as the *threshold of difference*. Visual acuity, or the power of distinguishing between the intensity of two lights, is greater in proportion as the value of the differential fraction is less. Innumerable careful researches have proved that the differential fraction is not a constant, as required by Weber's law, but varies considerably according to the absolute magnitude of the luminous stimulus.

The typographical tables used for determining visual acuity are modelled upon those of Snellen, and are so constructed that if the subject has normal sight, *i.e.* visual acuity = 1 (V = 1), he is able to read the smallest letters of the scale at a distance of 5 m., and the others, which are increasingly larger, at corresponding distances of 7·50-10-15-20-30-40-50 metres. The visual acuity is indicated by a fraction, which is obtained by taking as numerator the figure that indicates the distance at which the letters of the table can be read, and as denominator the figure that indicates the distance at which the smallest letters of the table which the subject is able to recognise can be read by a normal eye. If he can only recognise at a distance of 5 m. the letters

which ought to be plain at a distance of 15 m., his visual acuity is expressed in the fraction $\frac{5}{15} = \frac{1}{3}$.

The test is carried out as follows: The patient is placed at a distance of 5 m. from Snellen's type, and one eye at a time is examined, while the other is cut out by an opaque screen. Occlusion of the eye by the hand or by closing the muscles of the lid should be avoided, because in the subsequent examination this eye would then appear to have less visual acuity than is actually the case. Before commencing the experiment any ametropia must be corrected in the patient by means of concave, convex, or cylindrical lenses. He is then asked to read off the letters of the table beginning with the largest: the smallest he is able to read give the measure of his visual acuity, the arithmetical expression of which is shown by the numerals marked at the end of, or below, each row of letters.

The excitation of the retina and the sensation evoked are further dependent on the *duration* of the luminous stimulus. When this is too short, no sensation results unless the intensity of the stimulus is excessive—as with a flash or electric spark, which is perceived by the eye even if it lasts for an immeasurably short time.

Whether retinal activity is preceded by a brief latent period has not been, and perhaps cannot be, demonstrated, but it is known that a certain time (from 0·07 to 0·16 sec.) elapses after the commencement of the action of light before the visual sensation reaches its full intensity. For this reason, a bright light acting for a very short time seems less vivid than the same light acting for a longer time. After reaching its maximum by a certain curve —called by Fick and Exner the curve of rise or waxing (*Anklingen*) —the sensation remains constant for a longer or shorter period. This is the period best known to us, because it lasts the longest, and our attention is usually given to it. The climax of intensity is usually succeeded by a period of fall or waning (*Abklingen*), which only appears when we continue to look steadily at the source of light. When the light ceases to act the sensation disappears gradually after a certain time. This is the period of *after-effect*, which again declines progressively, and is the cause of *positive after-images*.

The phases of visual sensations during the action of light, and their persistence after the stimulus has ceased, can be demonstrated by a very simple experiment with rotating discs. The disc represented in Fig. 173 contains the same number of white sectors, which reflect a great deal of light, and black sectors, which reflect very little light. When it is rotated at a low velocity the white and black sectors are seen distinctly. But on increasing the speed of rotation the edges of the sectors become blurred. This proves that the sensation of black or white does not reach its maximal intensity at once, but only after a certain lapse of time (waxing phase); also that at the close of either stimulus the corresponding sensation does not cease suddenly but persists for a certain time (waning phase).

If the velocity of rotation is further accelerated, the clear sensation of alternate white and black ceases, and the brightness of the disc assumes a mean value of intensity oscillating between white and black (grey). This shows that the sensations of white and black no longer have the necessary time to reach their maximal intensity, owing to the speed at which the stimuli appear and disappear.

If the velocity of the rotating disc is still further accelerated the apparent variations in its luminosity cease, and it appears uniformly grey. In this case, according to Talbot's law, the luminous sensation should be the same as if the total action of the light were uniformly distributed in time. In practice, however, the disc of white and black sectors is not of equal light intensity at all velocities of rotation, but (according to Brücke) is a brighter grey when its revolutions amount to 17-18 per second. This striking deviation from Talbot's law depends on the varying ratio between the duration of the successive stimulations and the duration of the rising and falling phases of the excitations. Schenck further observed that if the white and black are not regularly distributed over the sectors of the disc a higher velocity of rotation is required to obtain fusion of the two sensations.

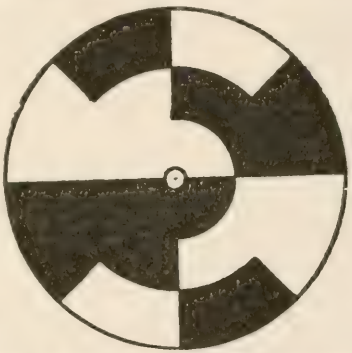


FIG. 173.—White and black disc of Helmholtz.

When the sensations of white and black are not fully fixed, that is, when the speed of rotation is moderate, "flicker" sensations can also be observed, in which all the colours of the spectrum are visible. White light can therefore be subjectively broken up into its components by means of a rotating disc with white and black sectors, without recourse to prisms or similar apparatus. This is an interesting point, as it shows the complicated nature of the conditions which determine the reaction of the retina.

To explain it we must start from the fact that for the simple colours of the spectrum, as well as for white light, a certain time is required before the retinal excitation can attain its maximum. The subjective decomposition of white light by the rotation of white and black discs can easily be explained on the assumption that the waxing and waning phases of sensation excited by rays of different wave-length are of different duration. It is only by assuming this that we can interpret the flicker sensation of colours in rapid succession when the velocity of rotation of the disc is moderate.

That the different spectral colours require different periods to produce maximal excitation in the retina is shown by the fact that the spectrum appears colourless and shortened at the red end, when presented to the eye for a very brief period. If the exposure is slightly prolonged it appears to consist only of a red and a blue portion. According to Kunkel's delicate researches, the red rays exert their maximal effect most rapidly, next the blue, and more slowly still the green rays.

The relatively slow course of retinal excitation explains a whole series of facts of common observation. The phases of waxing and waning of sensation explain why on glancing quickly round, or on gazing steadily at some one who is running, we are unable to distinguish the minute features of the objects or the several phases of the movement, and have only a confused and general impression.

After-effect explains why the rapid movement of a red-hot poker gives an impression of a fiery streak. By means of instantaneous photography it is possible to reproduce images perfect in every detail of the movements of one or more individuals as they come into the range of the camera. If these images are projected again, at the same speed at which they were photographed, a more or less complete reproduction of the scene is obtained, because the rapid succession of images fuses into a continuous, changing visual sensation. The Kinematographs, which have become so popular of late, are only an applied form of the physiological laws of the course of visual sensation—more exactly, of the after-effect of retinal excitation, and the resulting positive after-images.

These images are the more persistent, sharp, and intense in proportion to the strength of the luminous stimulation, and independently of its duration (Helmholtz). To obtain the maximal effect, the duration of the stimulus should not exceed $\frac{1}{5}$ sec. Persistent after-images follow exposure to a strong electric spark, the duration of which is infinitesimal. An after-image of the sun may last for some minutes, while that of a moderately illuminated object disappears after 2 secs. (Aubert).

Charpentier, by rotating discs, succeeded in determining the duration of the positive after-image under various conditions of illumination and duration of the luminous stimulus.

His results may be expressed as follows: with uniform duration of the light-stimulus the persistence of the positive image varies inversely with the illumination, approximately in inverse ratio to its square root. With uniform illumination, the persistence of the positive after-image varies inversely to the duration of stimulus, approximately in inverse ratio to its square root. So that increase in duration of stimulus acts, within experimental limits, as increase of illumination.

Persistence of luminous sensations after the stimulus has ceased occurs also when the retina is excited by lights of different colours. According to Charpentier, each colour acts in proportion to its luminous intensity. The positive after-image of a monochromatic light shows the colour of the stimulating light, which gradually fades till it disappears into the background.

Negative after-images, which result from fatigue of the elements of the retina, must be distinguished from *positive after-images*.

When a light object on a dark ground is fixated for a certain time (5-15 secs.), and the eye is then directed steadily to a larger surface which is uniformly bright and moderately illuminated, a part of this, which corresponds approximately to the form of the object fixated and to the portion of the retina excited, and therefore fatigued, appears dark in relation to the rest. This dark area, which reproduces the outlines and details of the object fixated the more plainly in proportion to the difference between its light and dark parts, is the *negative image* of it. It depends on the fact that the fatigued points of the retina are less excitable than the points which are not fatigued, or resting.

These negative after-images are common in daily life, but as they are incomplete, and our eyes are in constant motion, they generally escape notice. The duration of the negative images increases with the period of fixation and the luminous intensity of the object, and with the difference in illumination between the object and the background.

It is to be noted that after-images are relatively positive or negative, not absolutely so: the after-image of a very bright object is at the same time positive (bright) on closing the eyes, and negative (dark) on gazing at a well-illuminated surface.

The after-image of a bright object changes in absolute darkness from positive to negative, and afterwards a series of light and dark images alternate, until, after 4-5 minutes, the continuous sensation of a faint grey light alone remains. This is known as Plateau's oscillations of after-images, which had been previously described by Purkinje. They result from automatic variations of retinal activity, due to the periodical oscillations of its excitability, which are independent of the action of light.

VI. The positive and negative changes in visual sensibility, induced by different degrees of light or darkness, which Aubert termed *retinal adaptation*, are intimately connected with the phenomena of fatigue and recovery of the sensitive elements of the retina.

It is a matter of common observation that in passing rapidly from a good light into semi-darkness, one sees very badly at first, as though the darkness were total; after a time objects become indistinctly visible, and finally clearer, until after a few moments we are able to distinguish most details. This is known as adapta-

tion of the eye to darkness (*scotopia*), caused by the gradual recuperation and consequent increase of light sensibility in the retina.

The opposite effect is also an everyday experience. If after remaining a long time in the dark, or in semi-darkness, one passes suddenly into full light, the illumination—owing to the great sensitiveness of the retina—is at first so dazzling that it is impossible to see any object distinctly. Little by little, however, the retinal sensibility decreases from fatigue, and within a few minutes adaptation to light (*photopia*) is established.

Aubert, and more recently Piper, determined the curve of retinal adaptation to light in different people. Piper's results (1903) show that sensibility increases very slowly during the first 10 minutes in darkness; from 10 to 30-40 minutes the progressive increase is very rapid; from 30-40 up to 60-70 minutes the increase is again very slow, till the maximum of adaptation, *i.e.* of retinal sensitiveness, is reached.

The general character of the curve differs little with the individual; the degrees of sensitiveness, on the contrary, vary widely. This agrees with the common fact that the capacity for seeing with very weak illumination differs greatly in different individuals, even within physiological limits, quite apart from the pathological conditions known as *hemeralopia* or *night blindness*.

The increased functional capacity of the eye when adapted to darkness is always very considerable. According to Piper retinal sensitiveness to light may increase 1400-8000 times in the dark; but these values depend to a great extent on the size of the object and the quality of the light with which the threshold of sensibility is determined.

No special experiments have been made to discover the curve of progressive decline in retinal sensibility during light adaptation, but it is *a priori* obvious that it must vary to a large extent with the strength of the luminous stimulus. It is easy to verify the fact that light adaptation occurs much more rapidly than dark adaptation even for lights of moderate intensity, so that the eye soon attains its minimal sensitiveness.

Another fact that can be easily verified in the dark-adapted eye is that the increase of sensibility in the centre of the retina is much less than in its more eccentric parts. A delicate observation by Arago illustrates this fact. He noted that certain small stars, which are visible from the periphery of the retina by indirect fixation, become invisible as soon as they are viewed directly, so that their image falls on the fovea. A more direct proof of this was given by v. Kries. When, with the eye well adapted to darkness, we gaze in a room dimly illuminated by diffuse light at a black velvet field in which a number of small discs of white or blue paper are fastened, we can by looking aside (indirect vision)

distinguish them as faint shining dots on a black ground. But if we look at one directly we at once cease to see it, while the other discs, the images of which fall on the peripheral parts of the retina, remain visible. The more perfectly the eye is adapted to darkness the brighter will the objects appear with eccentric, and the less visible with central vision.

While, therefore, in day (photopic) vision, while the eye is adapted to light, the fovea centralis is the most sensitive part of the retina; in twilight (scotopic) vision, with the dark-adapted eye, the fovea is in a state of *physiological hemeralopia*, as compared with the peripheral parts of the retina. The progressive increase of retinal sensibility in the dark thus predominantly affects the peripheral zones, and only involves the central region of the retina to a much less extent.

Later on we shall return to the physiological value of this fact, which seems to be correlated with the formation of visual purple as found exclusively in the rods. But it may be added that these positive and negative variations of the sensibility of the eye to light afford an easy explanation of the everyday fact that we are able to tolerate considerable objective variations in the intensity of illumination without difficulty or inconvenience.

VII. It is an important fact that a stronger stimulus is required for *chromatic* sensations—*i.e.* to see and distinguish colours—than for *achromatic* or colourless sensations. Under weak illumination we can neither see nor distinguish the colours of objects: everything looks grey and obscure. The eye behaves as though it were totally colour-blind; and this is the characteristic of scotopic (twilight) vision.

Too vivid illumination also diminishes the power of discriminating colours; chromatic sensibility becomes increasingly fainter, and is finally lost; yellow readily passes into white.

It may therefore be said that clear, distinct chromatic sensations only occur with light of moderate intensity; with stronger or weaker light they become achromatic. This proves the uniform character of the light stimulus, considered objectively.

The relative brightness of colours, again, changes considerably with the degree of illumination. Yellow, orange, and red are the brightest colours in daylight, while with the same degree of illumination green, blue, and indigo appear comparatively dark. In twilight, on the contrary, yellow, orange, and above all red, become dimmed, while green and blue are relatively bright. This fact is known as Purkinje's phenomenon, as he first discovered it. It can easily be confirmed on looking at the spectrum of daylight or gaslight, under strong or weak illumination, with the eyes adapted to light or darkness.

On looking with light-adapted eyes at a well-illuminated solar spectrum, it is at once evident that the different colour-bands are

not equally distinct; the portion lying between Fraunhofer's *D* and *E* lines, between orange and yellow, stands out by its extreme brightness; passing from this region towards the red end or the violet end the brightness diminishes at first rapidly, then more slowly, then rapidly again. This difference in the luminosity of the colours of the spectrum is not due to differences in the energy of the ether vibrations of different wave-length, for we know that the thermal effects of the red rays, which are less bright, are greater than those of the yellow rays, which are brightest, and that maximal heat effects are obtained from the ultra-red rays, which are invisible. The difference in brightness depends, therefore, not on a different energy of vibration, nor on any objective difference in the respective monochromatic lights, but on the internal constitution of the receptor elements of the retina. The yellow rays are the brightest of all, because the receptors are more sensitive to these than to the other rays.

When the illumination is weak and the eyes are well adapted to darkness, the sensibility to rays of different wave-lengths is much altered. According to Hering and Hildebrand (1889), the spectrum then appears entirely colourless, and the relative brightness of the different bands is quite different from that in the strongly illuminated spectrum. While in the latter the maximal brightness lies between yellow and orange, that is, towards the less refrangible bands, and the minimal brightness in the more refrangible bands, in the weakly illuminated spectrum the maximal brightness lies between green and blue, that is, towards the more refrangible bands (which appear brighter than any others, in spite of their want of colour), and the minimal brightness lies in the red, the least refrangible band, which is sometimes completely invisible.

The colour sensibility of the light-adapted eye is not equal over the whole of the retina; it is greatest at the fovea, and decreases thence to the ora serrata. The most peripheral parts are quite colour-blind, and are only capable, therefore, of giving colourless sensations (Fig. 174). Between the fovea, in which sensibility to colour is maximal, and the peripheral parts of the retina, in which there is complete colour-blindness, lies an intermediate zone which is blind to red and green. In this area red and green lights appear to be a more or less saturated yellow, gradations of yellow being plainly visible, though this colour cannot be distinguished from either red or green. It is, however, to be noted that the inner and outer limits of this red-green blind area are only relative, and alter with the experimental conditions. When the size, photic intensity and chromatic saturation of the object are increased, these limits recede more or less towards the periphery of the retina. In fact, when an object is fixated by the intermediate area of the retina, and its size or luminous intensity is gradually increased from that at which it

is only just perceptible, it will be found that there is at first total colour-blindness, next red-green blindness, and lastly full sensibility to colour.

VIII. In 1866 Max Schultze founded the "duplicity theory" of the functions of the rods and cones, the end-organs of the optic nerve, by correlating the decline of colour sensibility from the centre to the periphery of the retina, with the diminution of cones and increase of rods between the fovea and the ora serrata.

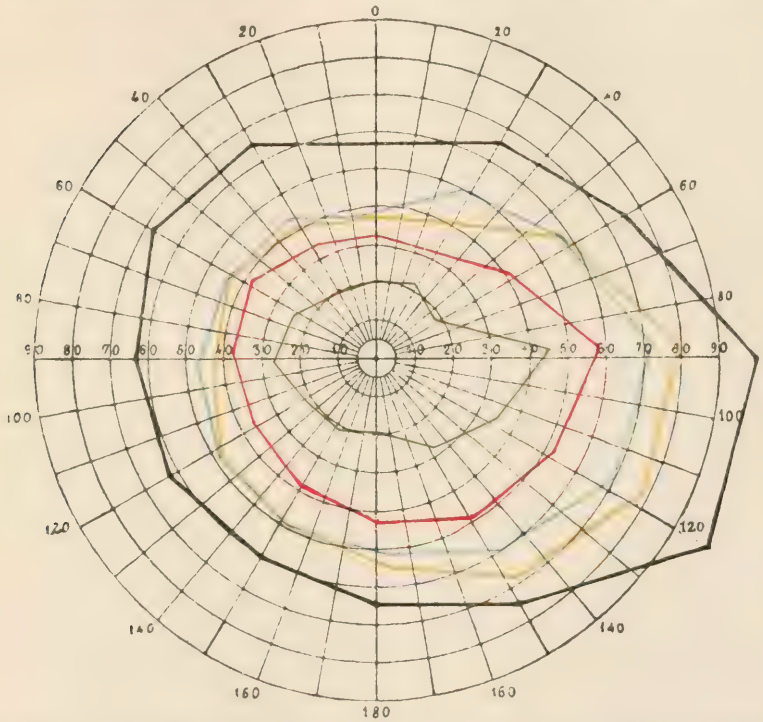


FIG. 174.- Visual field for white and the four principal colours, from right eye of a young physiologist, obtained with a test object 1 sq. m. under good illumination. (Baglioni.) The peripheral achromatic field is outlined in black, the coloured fields for yellow, blue, red, and green in the corresponding colours.

He concluded that the cones, which are the most highly differentiated elements of the retina, subserve light and colour perceptions, while the rods are concerned with the perceptions of light, but are incapable of initiating colour sensations.

In support of his hypothesis he pointed out the absence of cones in the retina of certain nocturnal animals (bats, moles, hedgehogs, and certain rodents); their relative paucity in some of the night birds, as compared with the mammalian retina in general, the cones in the day-birds being much more abundant

than in mammals; and finally, that in some species of reptiles that prefer bright light or the direct rays of the sun, as snakes, lizards, and tortoises, the retina consists almost or exclusively of cones.

Haab and Kühne held the same view, and also based it on the comparative predominance of rods and cones in the retina.

The observations of Parinaud (1884) and still more of v. Kries (1894) gave a wider basis to Schultze's theory. Von Kries assumed that the rods are the receptors in *scotopic* or twilight vision, and the cones, particularly those of the fovea, the organ of *photopic* or daylight vision. The characteristic differences in the physiological properties of the two systems form—according to v. Kries—the physical basis of the duplicity theory.

The characteristics of the scotopic system are:—

(*a*) Total blindness to colours, whatever the wave-lengths of the rays acting as stimuli, even when the retina is perfectly adapted to darkness.

(*b*) Preponderating sensitiveness to rays of medium or short wave-lengths; so that in the dispersion spectrum obtained through a prism the maximal brightness lies between green and blue, while red is quite dim.

(*c*) Retinal adaptation to darkness and consequent increase of sensibility to light, which preponderates in the peripheral as compared with the central portions of the retina.

(*d*) Capacity of the outer segments of the rods to form visual purple or rhodopsin, which, as it accumulates in the dark, is probably the sensitising substance.

On the other hand, the characteristics of the photopic system for daylight vision, which the cones subserve, are:—

(*a*) Appreciation of chromatic sensations, when stimulated by monochromatic rays of medium intensity.

(*b*) Appreciation of white, when stimulated by a mixture of light-rays, or by monochromatic rays of excessive or too low intensity.

(*c*) Visual acuity, which is maximal at the fovea, where only cones are present.

Certain objections have been raised to the theory of v. Kries, but they do not appear to invalidate the facts.

We have seen that the increase of retinal sensitiveness in the dark-adapted eye does not depend entirely on the rods, for when the fovea has been some time in the dark, it also exhibits a slight increase of sensibility to light. But this only proves, as v. Kries himself admitted, that adaptation does not depend exclusively on accumulation of erythropsin in the rods, which augment the sensitiveness of the entire retina, other factors being concerned. Doniselli regards it as probable that the slight increase of sensibility at the fovea is due to the marked increase of sensitiveness in the organ constituted by the rods.

Charpentier and Tschermak contended against the theory of v. Kries that in the fovea, unlike other parts of the retina in which rods are present, the absolute threshold value of the stimuli capable of arousing a luminous sensation coincides with the chromatic threshold, so that on starting from subliminal stimuli and gradually increasing their intensity, colour sensations with no interval of colourless sensations are at once perceived. But these observations do not overthrow v. Kries' theory, as he states that the cones, on stimulation by monochromatic rays of low intensity, give rise to colourless senations.

Hermann's objection to v. Kries' theory is still less conclusive. He contends that by it there must, in cases of *achromatopsia* or congenital colour-blindness, be a gap or *scotoma* in the visual field corresponding to the fovea—but this is not found to be the case. It is conceivable that in achromatopsia, owing to arrest of functional development, the cones may not have acquired the capacity of arousing colour sensations, but only have the power, common to the rods, of evoking simple colourless sensations. There are, however, as we shall see, cases of *achromatopsia with central scotoma*, which fully bear out v. Kries' theory.

On the other hand, in typical cases of colour-blindness, when light-adapted, the distribution of brightness in the spectrum corresponds approximately to that found in the normal dark-adapted eye, and is almost independent of the intensity of the stimulus. Moreover, eyes that are colour-blind are dazzled in full light, and their visual acuity is less than the normal average. All these facts agree perfectly with the hypothesis that achromatopsia is due to defective development in the functional capacity of the cones. But we shall consider this in detail, in reference to particular cases.

IX. Before putting forward any theory of colour-vision, it is necessary to discuss the phenomena which result from the mixture of colours.

Experience shows that, as a rule, mixtures of objectively different lights produce different effects upon the eye, and appear to us as different colours; often, however, subjectively equal lights or colours may be composed from mixtures of objectively different lights. The so-called *laws of colour-mixture*, which are of great physiological importance, have been obtained by methodical investigation of the conditions under which the different colours appear to us similar or different.

Simple or *homogeneous lights* or *colours* are those which result from ether vibrations of a known wave-length. We have seen that in the solar spectrum there is a series of imperceptible transitions from red to violet. Objectively, therefore, we should find an infinite range of simple hues, corresponding to the different wave-lengths or vibration-periods. Subjectively, how-

ever, there is no corresponding gradation of visual sensation. Our eye is only capable of distinguishing a limited number of colours and shades of colour (according to Schenck, about 200), each of which arises from a more or less extensive region of the spectrum, corresponding to a greater or less number of simple lights. The generally admitted distinctions of the spectral colours are more or less artificial. Aubert, Wundt, and others, however, distinguish four primary colours known in all the classical languages by specific, simple names (red, yellow, green, blue), as distinct from the intermediate colours which are designated by compound names (orange-yellow, yellow-green, blue-green, violet-blue, etc.). We shall find that Hering adopted this theory and arranged the four primary colours in two pairs of opponent colours (yellow-blue and red-green).

Retinal discrimination of shades of colour varies in the different parts of the spectrum. According to Dobrowolski, sensibility is maximal for yellow and blue, minimal for red and green.

The spectral colours are the purest it is possible to obtain: they are also the most saturated, that is the least diluted with white, when they result from rays of medium intensity.

It is otherwise with the colours of objects and the dyes or pigments used by dyers and painters, which result from the reflection of the rays that give the colour to the object, with simultaneous absorption of all other chromatic rays. The tone of these varies very much according to the smoothness of surface of the object, its transparency and the degree of absorption of the different chromatic rays. They are never saturated like the spectral colours, but always contain a greater or less amount of white.

Painters happily distinguish between warm colours and cold colours—expressions which have a real, and not merely a metaphorical significance. Orange and yellow are warm colours; blue, indigo, and violet are cold colours; green is an intermediate shade, warm if it inclines to yellow, cold if it verges on blue. Red and yellow are the colours of fire and of sunlight; blue and violet those of the weaker moonlight. Helmholtz observed that on looking through yellow glasses on a dull day the landscape assumes the aspect of sunshine; with blue glasses, on the contrary, the finest day presents the appearance of moonlight.

The compound light of an oil lamp, candle, or gas flame is usually very defective in blue and violet rays, and diffuses a warm tone of colour. The electric arc light, on the contrary, is rich in these rays, and diffuses a cold, bluish tint.

Newton first synthetised white light, by mixing the different chromatic rays that had been analysed by the prism, and formulated the most universal laws of colour-mixture; Graumann

reduced them to a stricter and more accurate formula; to Helmholtz we owe the complete, systematic study and experimental demonstration of these laws.

Just as the decomposition of white light yields all the hues and colours perceptible in the spectrum, so by the mixture or superposition of certain spectral colours in varying proportions we can artificially obtain all the more or less complex hues of nature.

The *physical method* is the most perfect means of obtaining colour-mixtures, and consists in allowing rays of different wavelength, previously separated by two prisms, to act simultaneously upon the retina. The application of this method involves a complicated apparatus which is described in all Text-books of Physics.

The *physiological method* is simpler, and consists in letting the colours to be mingled fall on the eye in succession instead of simultaneously, at such a rate that the persistence of the images causes superposition or mixture of the colours on the retina. Pigments can be used for this purpose instead of spectral colours, for though less saturated than the latter they contain the different tones of colour.

Various contrivances have been employed to obtain a physiological mixture of pigment colours. The most ingenious and that usually adopted is known as Maxwell's colour-discs. As shown by Fig. 175, these are circular papers of different colours—as opaque and as saturated as possible—with a radial slit, by which they can be superposed so as to present two or three differently coloured sectors, the area of which can be varied at will by the experimenter. These are placed on a metal disc, fixed in the centre by a screw, and are then rotated by clockwork; the visual sensation thus produced varies according to the colours employed, their saturation, and the relative proportion of the sectors upon the disc.

The mixture of two or more spectral colours produces a new colour, or rather a new visual sensation, which does not merely result from the superposition of the two component chromatic sensations, because the new colour is always less saturated than its two components. The luminous intensity is not diminished in the mixture, but part of the chromatic quality disappears, and is replaced by white.

When two colours of the spectrum known as *complementary* are mixed, all chromatic quality in the sensation disappears, and white or grey light only is perceived. This is the fundamental law of colour-mixtures, and it claims our attention in the first place.

Helmholtz demonstrated that not merely can white or grey light, *i.e.* colourless sensation, be obtained by mixing one or more

pairs of spectral colours, but that each ray of a given wave-length has as its complement another ray of the spectrum. Accordingly there is an infinite series of pairs of complementary colour-rays, *e.g.*—

Red has as its complement . . .	blue-green.
Orange has as its complement . . .	blue.
Yellow has as its complement . . .	indigo.
Yellow-green has as its complement . .	violet.

Green alone has no complementary colour in the spectrum, but its chromatic quality can be neutralised by a mixture of red and

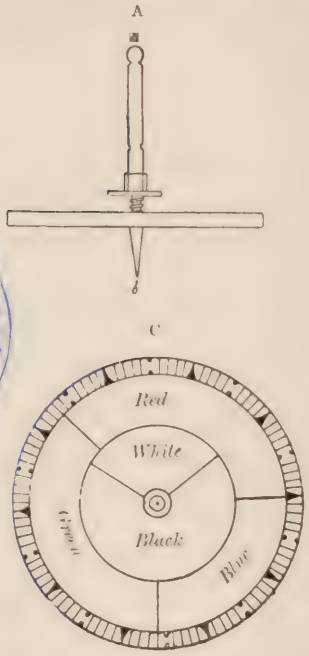


FIG. 175.—*A*, Maxwell's colour-discs, which can be rotated by clockwork; *B*, a disc of coloured paper, with a slit which allows the partial superposition of other discs of different colours, so as to obtain an area with variable, coloured sectors; *C*, metal disc surrounded by a graduated circle which enables the angular dimensions of each coloured sector to be read; the superposed coloured discs (red, green, blue) are fixed at the centre by a screw, with two smaller discs (white and black) to produce the different gradations of grey.

violet. As the colour purple is obtained by mixing the two ends of the spectrum, it follows that the complementary colour of green is *purple*. Young and Helmholtz regarded red, green, and violet —that is, the extremes and the central colour of the spectrum— as the fundamental colours and all the other spectral colours as intermediate. On this they based their theory of colour-vision (*infra*).

It follows that white light can be obtained not only by the simultaneous action of all the visible rays of sunlight, but also by the admixture of an indefinite number of pairs of simple colours with a definite difference of wave-length.

Our eye cannot distinguish between the objectively different

kinds of white light: as the white that results from the mixture of all the colour-rays of the solar spectrum from that produced by a mixture of red and blue-green, or from orange and blue, etc. None of these white lights present qualitative differences to vision, but, at most, simple quantitative differences due to the different intensities of the light, so that some appear to us more or less pure white or more or less grey. The eye thus differs fundamentally from the ear, since it is unable to analyse light; it cannot resolve the different mixed colours into the simple spectral colours of which they are made up, nor differentiate the various kinds of white light obtained by mixing different pairs of complementary colours. This, however, is no imperfection, but merely a physiological necessity of the visual sense. Otherwise we should be unable to see objects as white or variously coloured, but should only perceive a confused medley of different colours in every object.

When two spectral colours that are not complementary are mixed, the result is not white, but a new colour, which is always less saturated than the two components. This may be further analysed: the two colours to be mixed may be separated in the spectrum by a greater or less distance than the two complementary colours. In the first case the mixture produces an intermediate colour, which is paler as the distance in the spectrum between the two component colours is greater—more saturated as the distance is less. In the second case the mixture produces a colour which is more saturated in proportion as the distance of the two components in the spectrum is greater, paler as it is less (Helmholtz).

The following table gives the results of the different mixtures of spectral colours according to Helmholtz. The intersections of the vertical and the horizontal columns show the compound colours or white that result from the respective mixtures.

	Violet.	Indigo.	Light-blue.	Blue-green.	Green.	Yellow-green.	Yellow.
Red	Purple	Dark-pink	Pale-pink	*White*	Pale-yellow	Orange-yellow	Orange
Orange	Dark-pink	Pale-pink	*White*	Pale-yellow	Yellow	Yellow	
Yellow	Pale-pink	*White*	Pale-green	Pale-green	Yellow-green		
Yellow-green	*White*	Pale-green	Pale-green	Green			
Green	Pale-blue	Sea-blue	Blue-green				
Blue-green	Sea-blue	Blue					
Indigo	Indigo						

X. Closely related to the theory of colour-mixture are the phenomena of *coloured after-images*, described by Peiresc (1634), and *colour-contrast*, already known to Leonardo da Vinci (1519).

Positive and negative after-images have already been discussed from the point of view of luminous intensity or brightness, but without regard to their colour-tone. We must now consider *coloured after-images.*

Generally speaking, after fixating it for a few seconds, a coloured object yields an after-image which may be *positive, i.e.* of the same colour, but is more often *negative, i.e.* of the complementary colour—blue-green after red, violet after yellow, blue after orange, and *vice versa.*

If the eyes are first kept for a few moments in complete darkness, to increase the sensitiveness of the retina, and to obviate the after-effects of all previous impressions, and are then opened suddenly in daylight and then closed again, a positive after-image of external objects appears. If while the image is still plainly visible the eyes are again opened, and directed upon a white surface, the *positive* is transformed into a *negative* image, and assumes the complementary colour of the object fixated.

According to Fechner the positive *homochromatic* image (*i.e.* of the same colour as the light that induces it) seen in the dark is due to the persistence of the chromatic excitation, and the complementary negative image seen on exposure to white light is due to fatigue of the retina to the inducing colour, with unaffected excitability to all other colours of the spectrum—in the admixture of which the complementary colour predominates over that to which the retina has been fatigued. Johannes Müller had previously given a similar interpretation of this phenomenon.

White light, too, when it acts intensely on the retina produces coloured after-images, which alternate from red to green, and appear and disappear at a certain rhythm—a phenomenon described under the name of *coloured phases of the after-images.* They may be regularly observed on looking fixedly for a few seconds, with the dark-adapted eye, at a window on which the sun is shining, or at the bright light of a lamp. This phenomenon has been adequately described by Fechner, Séquin, Plateau, Helmholtz, and others; it occurs not only with white light, but also with brightly illuminated saturated colours, although their phases are not so definite.

Various hypotheses have been suggested in explanation. Generally speaking, it may be said that after vigorous stimulation the excitability of the retina to various colours passes through a series of positive and negative oscillations; the cerebral visual centres consequently receive alternate impulses which determine complementary colour-sensations and periodic appearance and disappearance of the images.

It may also be stated that, according to our present knowledge, after-images—whether coloured or colourless—are associated only with peripheral changes in the activity of the retina, and that no

cerebral after-images occur in the sense assumed by Bocci (1896) and other observers.

The fact from which Bocci assumed the existence of cerebral after-images is only the confirmation by improved methods of an experiment which Brewster made sixty years earlier.

If, in diffuse daylight, we look with the right eye for some time at a black figure in the middle of a white card, while the left eye is closed, the eye that is fatigued is apt to produce an after-image. But if we then close the right (fatigued) eye, and open the left (rested) eye, no after-image appears. When, however, the card is vividly illuminated by bright sunlight, on opening the rested eye the image of the figure reappears upon a more or less obscure field—and is bright red on a green background; this after-image exhibits the variations of the chromatic phases, with rhythmical waxing and waning. This is the image claimed by Bocci as "cerebral" because, in his opinion, it arises in the visual centres of the cortex, and is projected externally.

The same result may be obtained from a simpler form of this experiment. Thus, Ovio gazed for some moments at the sun with one eye, through a red glass. He then closed that eye and looked with the other at the white wall of a shaded room, and found it slightly tinged with red. This is the *positive* after-image, which seems to arise in the retina of the eye at rest, although the stimulus acts only on the other eye.

Baquis was the first who confirmed Bocci's experiment—and at the same time disproved his explanation of it. He maintained that the after-image which Bocci referred to the rested eye really originated in the fatigued eye, and was projected, as is always the case, into the binocular field of vision.

Baquis convinced himself of the accuracy of this view by the following experiment. On fixating the sun-lighted card, by Bocci's method, with the right eye alone, and then covering both eyes, the image of the figure is seen in glowing colours (usually red and green), and appears and disappears rhythmically. If the rested eye is suddenly opened while the image is in the field, a quite low degree of objective light will cause it to fade immediately. If both eyes are then again covered, and, after making sure that the after-image is still present, the rested eye is quickly opened again during the phase of disappearance, no image is visible. So that the rested eye sees nothing, either in the phase of return or in the fading of the after-image; and Bocci's after-image can consequently be referred only to the active eye, though it is projected into the binocular field.

Baquis further found that if, after stimulating the right eye by light in the usual way, both eyes were covered in a dim room, and the stimulated eye was reopened during a phase of appearance or disappearance, the image remained visible, or reappeared in the

field. It is obvious that no impulse originates in the rested eye, either in the phase of return or of fading, but that the image is present in the stimulated eye alone, and is only perceived there.

Gaudenzi instituted other experiments to confirm Baquis' conclusions, and showed that when, in persons who are wholly or partially blind in one eye owing to any kind of retinal lesion, an after-image is evoked in the sound eye, the disease of the other does not exclude or affect the appearance of Brewster-Bocci's after-image in the field of vision.

The most striking experiment in proof of the impossibility of explaining this phenomenon by any functional alteration induced in the rested eye is as follows: If in an individual in whom both eyes are normal an after-image is evoked from that part of the retina of the left eye which coincides in the right eye with the optic papilla (Fig. 176), then, on closing the stimulated eye and opening the other, the after-image appears in that part of the visual field of the rested eye which corresponds to Mariotte's blind spot—*i.e.* to a part where there is no retina, and to which, accordingly, no excitation can be transmitted eccentrically from the central nervous organs.

It is an interesting point that this crucial experiment was made almost at the same time, but independently, by Gaudenzi to refute Bocci's theory, and by Bocci himself to establish a fresh argument in support of his view. As the two observers came to identical results, the conclusion should agree also. Gaudenzi concluded logically that the after-image in question "could only originate from the physiological processes which affect the retina of the exposed eye in consequence of the primary excitation." Nothing more is wanted to explain the genesis of this phenomenon.

The effects known as *colour-contrast* are closely allied to those of the after-image. By "contrast" we mean the altered impression reciprocally produced by two different colours, when these are not superposed or mixed, but are presented to the eye successively or simultaneously in two distinct and adjacent fields. Chevreul (1839), who first studied this subject systematically, drew a distinction between *successive* and *simultaneous* contrast. Brücke gave the name of "induced colour" to that which is altered, or which appears on a colourless surface, of "inducing colour" to that which brings about the change.

Successive contrast depends largely upon negative after-images and their projection upon a dissimilar background. If after gazing for some time upon a small red square on a black ground the eyes are turned upon a white field, an after-image appears in the colour complementary to red (blue-green); if the gaze is now directed to a violet field, the after-image becomes blue; if to an orange field, yellow. Speaking generally, the colour of the region occupied by

the after-image is that which results from the mixture of the (complementary) colour of the after-image with that of the background on to which it is projected.

If the after-image is projected on to a background of the inducing colour, the part on which it falls appears dimmed or

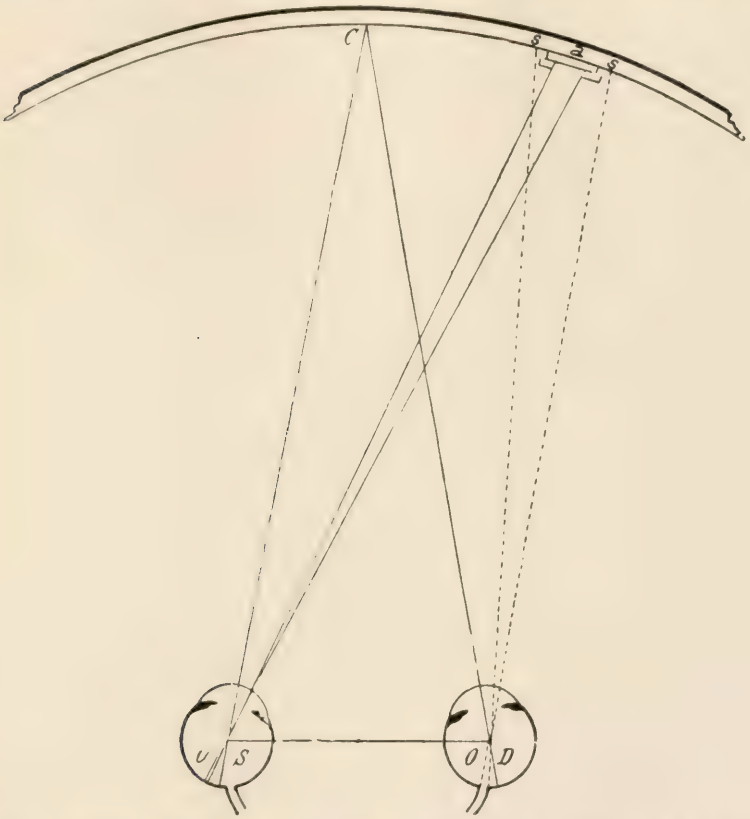


FIG. 176.—Gaudenzi's experiment for repetition and interpretation of Brewster-Bocci's "cerebra visual images." *OS*, uncovered left eye; *OD*, covered right eye; *C*, central point of perimeter fixated by the two eyes alternately; *ss*, position of physiological scotoma (Mariotte's blind spot) in the covered eye; *a*, position of a lamp, partially covered by a screen. When the head is fixed in the perimeter, point *C* is fixated with the right eye, and the limits, *ss*, of the blind spot of this eye are traced on the arc of the perimeter. Both eyes are then covered and the room darkened, to adapt the retina to darkness; after a few minutes the left eye is uncovered, and while fixated on *C* it is exposed for 20-30 seconds to the light of lamp *a*, so as to provoke a persistent image in a part of the retina corresponding to the optic papilla of the right eye. The left eye is then closed, and the right eye opened and fixated on the centre *C*; after a few seconds, Brewster-Bocci's image is seen in the region of Mariotte's blind spot.

grey; if, on the contrary, it is projected on to a surface of complementary colour the part it falls on appears brighter and more saturated. Generally speaking, the colours which are complementary or nearest to the complementary become more

saturated and brighter by contrast; colours which resemble the original or are very near it in tone are dulled and feeble.

The same effects appear even more plainly when a small square of the inducing colour is placed on a large surface of a colour that will be altered by contrast with the induced colour. After gazing at the square for a few seconds it is removed, and the contrast-colour may then be observed on the square which it occupied.

Under certain conditions the subjective contrast-colour may be so strong as to predominate over the objective colour upon which the after-image is projected. If, *e.g.*, a small square of dark orange paper is stuck in the middle of a red glass field, and the bright sky looked at through it, the intensity of the induced blue-green will be so pronounced that the orange square appears blue.

An experiment suggested by Johannes Müller is instructive owing to its simplicity. If, after fixating a red square on a white ground, the gaze is turned to one of the angles of the square so that its objective image R and the subjective after image V are partially superposed (Fig. 177), it will be seen that the greater part of R remains red, and the greater part of V assumes the green complementary colour, while the part in which the two images overlap appears to be pink shading into grey. This effect is the natural result of the fusion of the two complementary colours.

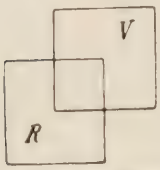


FIG. 177.—Joh. Müller's experiment on coloured after-images.

All the phenomena of colour-contrast can be repeated by Müller's device, using small squares of different colours on a background of the complementary colours or of a colour approximating to that of the square. In the first case the colour of the background is reinforced by contrast; in the second it becomes dim and pale.

The effects of *simultaneous contrast* are more difficult to interpret. It is well known to painters, whose colour-sense is specially developed, that two colours in juxtaposition affect each other. A grey figure seems brighter and more luminous on a black than on a white ground; a coloured figure seems brighter and more saturated when the complementary or contrast-colour predominates round it.

Under special conditions the phenomena of simultaneous contrast are surprisingly plain and obvious. One of the most interesting experiments is that of the so-called *coloured shadows*, already known to v. Guericke (1612) and Buffon (1743). When the shadows a, b, produced by two candles A, B, of a vertical rod or pencil c are thrown on to a white screen (Fig. 178), with a red glass in front of A, shadow b, which is illuminated only by

the flame of *A*, will be red, while shadow *a*, which is illuminated only by flame *B* and should therefore appear white, will look *green* by contrast.

This experiment may be varied by substituting daylight for one of the candle flames. In this case it is not necessary to use coloured glass, because daylight differs from candlelight in being white, not yellowish. Daylight casts a grey shadow, but on lighting the candle the grey shadow turns *yellow*, and the other shadow which is due to daylight appears *blue* by contrast.

In Ragona-Scinà's experiment the effect of simultaneous contrast is obtained by reflection. A black spot is observed through coloured glass, at an angle of 45°, and the glass is so arranged that the reflected image of another black spot is seen beside it; seen separately, the first spot will be the colour of the glass, the second black; viewed together, the second assumes the complementary colour of the first.

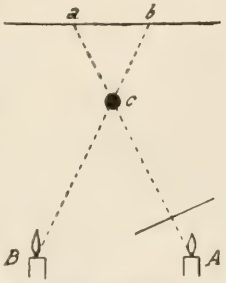


FIG. 178.—Experiment on coloured shadows.

Colour-contrasts are more easily obtained with pale than with saturated hues. This is readily demonstrated by the following experiment of H. Meyer. If a square of grey paper is placed on a sheet of coloured paper, its tint does not alter perceptibly; but if the whole is covered with a sheet of semi-transparent tissue-paper the small square assumes the complementary hue of the background: if the latter is red, it appears greenish; if yellow, bluish; if blue, yellowish; and so on. This striking effect proves that contrast-effects are much more pronounced when the colours are rendered less saturated by the addition of white.

Other analogous contrast-effects can be obtained by means of revolving discs. If black sectors with serrated edges are rotated on a white disc (Fig. 179), a series of concentric rings appear, which look darker from the periphery to the centre of the disc. The amount of black in each of these rings is constant, but owing to contrast each ring appears brighter at the inner part, next to a darker ring, and darker at the outer part, next to a lighter ring (Masson's experiment).

If instead of black sectors on a white ground two different colours are taken, then while the disc is rotating each ring shows different colours at its two edges, although the objective colour is uniform throughout each ring. If, *e.g.*, blue and yellow are substituted for black and white, the resulting rings are of different shades of grey, but each ring shows an inner yellow border, as contrasted with the preceding ring, which is bluer, and an outer blue border in contrast to the next and more strongly yellow ring.

When thin coloured sectors, interrupted in the middle by a band which is half black and half white (Fig. 180), are rotated on a white disc, the band should appear as a grey ring on a slightly tinted whitish ground. Owing to contrast, however, the ring is not seen as grey, but in the colour complementary to that of the coloured sectors.

This experiment, devised by Helmholtz, is only a proof in another form of H. Meyer's earlier experiment, which shows that simultaneous contrasts become plainer with pale colours in the presence of light grey. Instead of covering the grey square on the coloured background with semi-transparent tissue-paper, to dilute it with white, Helmholtz obtained the same effect by the physiological mixture of white and coloured and white and black segments, that results on rapidly rotating the disc.

From these examples it is plain that owing to simultaneous



FIG. 179.—Masson's disc for experiments on colour-contrast.



FIG. 180.—Helmholtz' disc for experiments on colour-contrast.

contrast a bright object placed beside a darker object becomes brighter and more luminous, and *vice versa*; and that a coloured object in the vicinity of another that is not coloured (white or grey) diffuses its complementary hue to the latter.

Helmholtz interpreted the phenomena of simultaneous contrast as errors of judgment. In the case, *e.g.*, of coloured shadows we mistake for white the yellow of the area illuminated by the candle, and consequently assume that the shadows which are really grey are bluish; Hering, on the other hand, showed by a variety of experiments that simultaneous contrast is not an error of judgment, but that it depends on the spread of excitation to the parts of the retina adjacent to those stimulated.

XI. Since the time of Aristotle a number of hypotheses have been put forward to explain the qualitative differences of visual sensation, that is, of the perception of colours. The more generally accepted theories of colour-vision are undoubtedly that of

Thomas Young (1807), which was taken up and perfected by Helmholtz (1852), of Wundt (1874–1902), and of Hering (1878). Schenck more recently (1906–8) formulated a new theory in which he attempted to supplement and reconcile those of his predecessors.

Young regarded the colours of the solar spectrum as the summation of different mixtures of three simple or fundamental colours—*red* and *violet*, the two extremes, and *green*, the middle hue of the spectrum. "It is certain," he wrote, "that the perfect sensations of yellow and of blue are produced respectively by mixtures of red and green and of green and violet lights, and there is reason to suspect that these sensations are always compounded of the separate sensations combined: at least this supposition simplifies the theory of colours: it may therefore be adopted with advantage, until it be found inconsistent with any of the phenomena; and we may consider white light as composed of a mixture of red, green, and violet only."[1]

On Young's original theory all colour-sensations are compounded from three fundamental sensations which are qualitatively constant, and only vary in intensity. To conform to the law of specific energy Young assumed as a subsidiary hypothesis that three kinds of receptor nerve-fibres are present in the retina at every point that can be stimulated by the three colours, to which three kinds of perceptor elements for red, green, and violet correspond in the brain-centres.

Against Young's theory is the fact that it is not possible by the mixture of these three colours to reproduce all the tones and saturations of the colours of the spectrum—mixed colours being always less saturated than their components.

Helmholtz easily disposed of this and other difficulties by assuming that each fundamental colour is capable of stimulating the three hypothetical receptor elements, but in different degrees, according to the difference of wave-lengths. Light of longer wave-length chiefly excites the elements that are sensitive to red; that of intermediate wave-length, the elements sensitive to green; that of short wave-length, the elements sensitive to violet.

If the colours of the spectrum from red to violet are arranged in horizontal series, the three curves (Fig. 181), according to Helmholtz, approximately represent the excitability of Young's three specific nerve-elements. The red rays (R) stimulate the red elements strongly, the other two elements weakly; the same applies to the green (G) and violet (V) rays; and this accounts for the sensations of red, green, or violet.

On this presumption the sensation produced by the red of the spectrum must include that of *white*, which results from weak,

[1] *Lectures on Natural Philosophy*, by Thomas Young, 1807. XXXVII. "On Physical Optics," p. 439.

simultaneous stimulation of the green and violet elements. In fact, on looking at spectral red when the green and violet elements have been fatigued by prolonged stimulation by the complementary colours (blue-green) the sensation of red appears more saturated than before.

Mixed colours are less saturated than their components because they result from the unequal stimulation of the three receptor elements. White is the result of the approximately equal stimulation of the three elements; grey is only white, feebly illuminated; black is white with the least possible degree of illumination. So that between black, grey, and white there is no qualitative but only a quantitative difference. The transformation of a coloured sensation into white owing to increased intensity of light is explained on the assumption that in this case the excitation of the three separate elements is at its maximum.

Inasmuch as the stimulation of the receptor apparatus of the

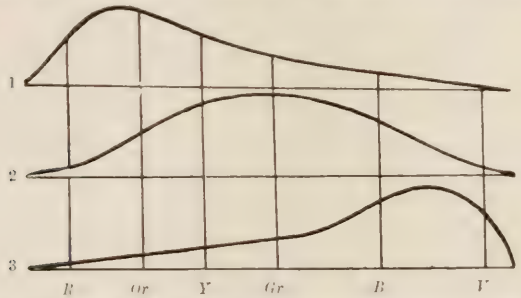


FIG. 181.—Excitability-curve of the three fundamental components of colour-vision. (Helmholtz.) 1, for red; 2, for green; 3, for violet rays. Abscissa = colours of the spectrum in their relative positions.

retina by light most probably consists in chemical changes, v. Helmholtz, in the second edition of his *Physiological Optics* (1889), modified his theory by substituting for Young's three nerve-fibres three kinds of photochemical substances, with which each receptor element in the retina that is capable of giving rise to coloured sensation must be provided. In the cerebral cortex three different kinds of perceptor cells must correspond to the three substances sensitive to the red, green, and violet rays.

As a working hypothesis Helmholtz' theory has done good service in countless experiments on vision: it is also simple and helps to explain many phenomena. It does not, however, interpret all the facts, and many objections have been raised against it.

Why, as Fick remarked, should *violet* be taken as the third fundamental colour? It is obvious that there is a less qualitative difference between red and violet than between red and green and between green and violet. The three primary colours must be chosen so as to make the difference between them, respectively,

as equal as possible. It would consequently be better to take dark blue instead of violet for the third colour, as did A. Fick and König. With red, green, and blue we can obtain all the intermediate colours of the spectrum, which is not possible with red, green, and violet.

It was long supposed that Young's three-colour theory was supported by facts observed in partial colour-blindness (*dyschromatopsia*). Helmholtz assumed three different kinds of dyschromatopsia—red-blindness (*anerythropsia*), green-blindness (*achloropsia*), and violet-blindness (*acyanopsia*)—due to deficiency of one or other of the three receptor substances. But more accurate and comprehensive study of these cases has shown the impossibility of explaining them on this theory. As Wundt pointed out, it is inadequate to explain cases of total colour-blindness (*achromatopsia*) in which the solar spectrum appears colourless, brightest in the middle (in the yellow-green), and less bright at the ends, while paintings appear as photographs. Again the fact that in red- and green-blindness white light appears white and not coloured, as it should according to the Young-Helmholtz theory, is irreconcilable with it. The colour-blind, moreover, declare that they see yellow and blue, while on this theory they should see green and violet (*anerythropsia*) or red and violet (*achloropsia*).

To obviate this and other difficulties inseparable from the three-colour hypothesis, Wundt, as early as the first edition of his *Psychological Physiology* (1874), brought forward another theory based on the assumption that two different stimulation processes, *chromatic* and *achromatic*, are set in action by every retinal irritation. The chromatic excitation is a function of the wave-length of the vibrations; the achromatic is a function of the amplitude of the vibrations.

Chromatic stimulation, according to Wundt, is a *polyform photochemical process* which changes with the wave-length; achromatic stimulation, on the contrary, is a uniform *photochemical process*, which changes only in intensity and not in quality with alteration of the wave-length.

Achromatic excitation can be aroused by the weakest and the strongest stimuli; chromatic excitation can only be evoked by stimuli of moderate intensity. Wundt assumed that achromatic sensations preceded chromatic sensations in the phylogenetic and ontogenetic development of vision, and were not therefore the product of the latter.

Wundt's hypothesis is obviously too vague and indefinite, and scarcely deserves the name of a theory. Have the achromatic and chromatic excitatory processes any distinct physiological substrate in the retina? This could be answered by means of the "duplicity theory" which Schultze, Parinaud, and v. Kries put forward in regard to the functions of the rods and cones. Is it,

however, possible to conceive the chromatic excitations of the cones as dependent on a polyform photochemical process, which alters with the wave-length of the vibrations, without assuming the presence of an indefinite number of chemical substances that differ specifically, inasmuch as they are exclusively sensitive to rays of a given wave-length?

Yet, notwithstanding its indefiniteness at this crucial point, Wundt's theory must be given the credit of having clearly pointed out that achromatic sensations arise from simple primitive excitatory processes and are entirely independent of the chromatic sensations that are developed later.

Hering's theory of colour-vision, which, after that of Young-Helmholtz, has been most widely accepted by physiologists, has many points of resemblance with Wundt's theory, particularly in assuming achromatic to be independent of chromatic perception; but it differs fundamentally in seeking to apply Johannes Müller's law of the specific energies, by reducing the fundamental qualities of visual sensation to six—white, black, red, green, yellow, and blue.

Hering assumes that there are three different photochemical visual substances in the sensory elements of the retina, which are continually broken down and built up again, like Boll's visual purple. One of these substances is the physiological substrate of achromatic sensations, *i.e.* black and white; the other two give rise to chromatic sensations. He replaces the three primary colours of Young-Helmholtz by the four principal colours of the spectrum (already recognised by Aubert, and much earlier by Leonardo da Vinci), viz. red, yellow, green, and blue, which he arranges in two pairs of opponent colours—red-green and yellow-blue, to each of which he assigns a specific photochemical visual substance.

Two antagonistic and simultaneous processes, the one assimilative or anabolic, the other dissimilative or katabolic, are constantly taking place in the three kinds of visual substance.

When dissimilation prevails, sensations of white, red, and yellow (katabolic sensations) are excited; when assimilation predominates, the sensations are black, green, and blue (anabolic sensations); when the two opponent processes balance (autonomous equilibrium) there is a sensation of grey (mixture of black and white) or white (mixture of the antagonistic pairs), by which the colours are annulled. On these elaborate studies of vision Hering founded his general theory of the metabolism of living matter (Vol. I. pp. 42, 86).

Hering assumes that the retina contains more of the white-black than of the red-green and yellow-blue substances. Consequently the assimilatory and dissimilatory changes are more conspicuous in the first achromatic substance than in the two

other chromatic substances. This explains why coloured sensations only occur under special favourable conditions, and are usually associated with simultaneous colourless sensations which diminish their saturation.

All rays of the visible spectrum excite dissimilation in the white-black substance, but in a different degree according to their wave-lengths. In the yellow-blue and red-green substances, on the contrary, some rays excite dissimilation, others assimilation, others again produce no effect.

The extent of the katabolic or anabolic change in each of the three visual substances depends not only on the intensity of the stimulus, but also on the excitability of the substances. This explains why the same objective mixture of light-rays may appear lighter or darker, coloured or colourless, according to the "tuning" (*Stimmung*) or functional state of the retina.

Hering only admits two forms of partial colour-blindness—red-green and yellow-blue blindness, according as one or other of the chromatic visual substances is defective. If both are absent, the colour-blindness is total.

This theory, which Hering terms that of the "opponent colours," has elucidated many facts that are of value in the interpretation of colour-vision, but when critically examined it leaves a number of obscure points unexplained. Von Kries, for instance, pointed out the existence of two distinct types of red-green blindness which cannot be explained either by the Young-Helmholtz or by the Hering theory. There are also different types of total colour-blindness which cannot be adequately interpreted on these theories.

Schenck accordingly propounded another hypothesis which combines certain points of the theories of Young-Helmholtz and Hering, while it provides a physiological explanation of the various forms of colour-blindness—whether partial (*dyschromatopsia*) or total (*achromatopsia*).

XII. Schenck's theory of colour-sensations and colour-blindness is, as he expressly states, a revival, development, and elaboration of the theory of colour-perception in indirect vision put forward by his master, A. Fick (1879–1900). It may be termed the "developmental theory" of colour-vision.

Schenck accepted the three primary colours of Young-Helmholtz as adequate for fully-developed colour-vision. Like Fick, he substituted blue for violet, since it is possible with appropriate mixtures of red, green, and blue to obtain any other quality of colour-sensation. Three specific visual substances correspond to the three fundamental sensations, and are excitable, respectively, by the vibrations of long, medium, and short wave-length, as was assumed by Helmholtz.

Schenck adopts Tschermak's division of each of the three visual

substances into two parts—a stimulus-receptor (*Reizempfänger*) and a sensation-stimulator (*Empfindungserreger*). Schaum suggested that the receptors act as optical sensitisers of the cones, as visual purple is the sensitiser of the rods; Richarz, that they may be regarded as optical resonators for light of short, medium, or long wave-length. The mechanism by which the stimulators transform the optic resonances into physiological stimuli of the nerve-fibres is unknown, but when these are conducted to the central nervous organs they give rise to achromatic and chromatic sensations. The rods contain one stimulator, for white; the cones contain three, for red, green, and blue.

Even with this modification the Young-Helmholtz theory does not adequately explain why the sensations of white and yellow—which for physiological and psychological reasons are regarded by Wundt and Hering as simple sensations—are not connected with as simple physiological processes as the sensations of red, green, and blue. To remove this difficulty Schenck assumes that this connection between the sensations of white and yellow by simple physiological processes actually exists in the early phases of development of the visual organs.

According to Schenck, the cones which subserve the perception of brightness or luminosity—and which, on the well-established view of v. Kries, constitute the only organ capable of colour-vision—contain at an earlier developmental phase one substance only, which, on stimulation, gives the sensation white. This primitive visual substance is allied to the visual substance of the rods, which subserves scotopic vision, as it is little sensitive to light of long wave-length.

Later on, the primitive visual substance undergoes a change which makes it more sensitive to light of longer wave-length, which Schenck—on analogy with photographic nomenclature—calls *panchromatisation*, but it still continues to be the substrate of white light vision.

At a further stage of development there is a cleavage of the primitive visual substance, and *pari passu* a differentiation of its two parts and of their function. This cleavage occurs at two distinct periods:—

(*a*) In the first place, two visual substances are formed from the original white substance, one of which is specially sensitive to vibrations of long wave-length, and gives rise to the sensation of yellow; the other is more sensitive to vibrations of short wave-length, and excites the sensation of blue. But when equally and simultaneously stimulated, they still give rise to the sensation white, as did the mother-substance before its differentiation into two parts.

(*b*) Later again, by an analogous process, the yellow substance becomes differentiated into a red and a green substance, which

when equally and simultaneously stimulated arouse the sensation of yellow.

On this theory typical cases of congenital colour-blindness, total or partial, are readily explained by assuming that owing to some arrest of development panchromatisation, *i.e.* subdivision of the primitive substance which on stimulation gives rise to the sensation white, is wholly or partially defective.

Schenck's theory explains the different visual sensibility of the different areas of the retina. We have seen that the central fovea is sensitive to all colours, the intermediate region blind to red and green, the periphery entirely colour-blind; also that the limits of the intermediate zone which is blind to red and green are not fixed, but alter according to the conditions of experiment; on increasing the size, luminous intensity, and saturation of the test-object, the limits extend outwards.

These facts, which point to a functional differentiation between the central and peripheral parts of the retina in regard to colour-vision, can be explained on the assumption that panchromatisation is less advanced in the periphery than in the centre of the retina. But as the differences are relative, not absolute, it would, says Schenck, be fallacious to conclude that the more peripheral cones contain only the primitive white substance, and that others in the middle zone are in the first stage of panchromatisation, and others again, in the centre, are completely panchromatised.

It agrees better with the facts to assume that in the adult retina each cone contains all three chromatic substances, but in varying degrees of excitability, according to their relative positions, so that some are more sensitive to stimulation than others; like the different sensitive layers of a photographic plate. The fact that the area of peripheral colour-vision is larger when the size, luminous intensity, and saturation of the colour of the test-object are increased is parallel to the sensibility for white light, and is explained by assuming that adjacent cones have a reciprocal influence which favours the spread of excitation. The accurate work of Hess (1889) and of v. Kries (1904) showed that two lights of different colour, whether compound or homogeneous, which are of equal intensity when they fall on the centre of the retina, are also equally bright to every peripheral part of it. Moreover, other conditions being equal, any light appears uniformly bright to the different retinal areas, whether it is seen coloured by the central part or colourless with the more peripheral portions.

These facts, which prove uniformity of vision in the centre and the periphery of the retina, are adequately explained by Schenck's theory, which assumes that each visual substance consists of two parts—one to receive and transmit the stimulus, the other to excite the sensation. The first determines brightness, the second colour; the first explains the equal sensibility to brightness of

the different parts of the retina, the second the differences which they present in regard to colour.

The different forms of total and partial colour-blindness, which resist interpretation on Hering's theory, can be rationally explained by Schenck's hypothesis as follows:

(*a*) The *deuteranopia* of v. Kries (erroneously known as "green-blindness") is a reduction-system from normal colour-vision. It agrees thus far with the red-green blindness of the middle retinal zone, that affected people describe only white, yellow, and blue sensations, and have no sensation of red, which is perceived as yellow, or of green, which seems colourless. The deuteranopic differs from the normal eye in that the red-green blindness is not confined to the middle zone, but extends to the central part of the retina, and does not disappear on increasing the area, intensity, and saturation of the object.

On Schenck's theory deuteranopia is explained quite simply by assuming that owing to arrested development in the cones the second phase in the cleavage of the yellow substance into the red and the green substance has not taken place.

(*b*) The *protanopia* of v. Kries (erroneously termed "red-blindness") is a reduction-system, which differs from deuteranopia by a different distribution of spectral luminosity, but is practically identical with it in all other respects. Protanopes, according to v. Kries, show diminished sensibility to light of long wave-length, so that the more highly refractive part of the spectrum is shortened, the red appears very dark, and the yellow less bright than in normal individuals. The sensibility to light of short wave-length —from about 500 to 391 $\mu\mu$, or from the end of the yellow to the end of the violet—appears, on the contrary, to be relatively greater in protanopes than in deuteranopes and normals. So that while red seems much darker to protanopes, green and blue are rather brighter to them than to normal people.

To explain protanopia on Schenck's theory it must be assumed that the receptor or resonator for rays of long wave-length is absent, while the stimulator of red sensations is present; and that the second phase in the cleavage of the primitive visual substance has not taken place.

(*c*) *Blue-yellow blindness* is a rare form of congenital dyschromatopsia. Up to the present four cases only have been fully investigated. Individuals who are blind to blue and yellow describe only three light-sensations—white, bluish-red, and bluish-green. They call the lights which normals see as white, yellow, and indigo-blue *white*; the light of long wave-length *red*; that of medium wave-length *green*. Like normal individuals they recognise the uniform luminosity of different homogeneous or mixed lights, as well as the varying brightness in the different parts of the spectrum. We may therefore conclude that in this form of partial

colour-blindness there is no deficiency in the cones of the substance on which the luminosity of the light depends (receptors), but, as in deuteranopia, there is a reduction in the number of the sensations aroused by the stimulators.

On Schenck's theory blue-yellow blindness can be explained as due to anomalous development, in which the second phase in the cleavage of the primitive substance reaches a certain stage without the first having taken place.

(*d*) *Total colour-blindness* (*achromatopsia*), which is normal to the most peripheral part of the retina, may under various abnormal conditions, congenital or acquired, extend over the whole retina.

One form of achromatopsia depends on functional absence of the cones, while the rod-functions persist. In this the distribution of brightness in the spectrum coincides with that observed in scotopic vision and where there is a central scotoma. Several clinical cases have been well investigated, and afford complete confirmation of v. Kries' duplicity theory of the functions of the rods and cones.

A second variety of achromatopsia differs from the preceding only in there being no central scotoma. These cases are well explained on Schenck's theory by assuming that the evolution of the cones became arrested at the first stage when only the primitive visual substance was present, before it had undergone cleavage; consequently the sensation of white light is alone perceptible.

A third variety of achromatopsia is characterised by that distribution of brightness in the spectrum which is observed in the outer zone of the retina in deuteranopes, due, on Schenck's theory, to the absence of receptors for rays of long wave-length. In two clinical cases examined by König the peripheral colour-blindness of protanopes extended to the centre of the retina. In one case there was total colour-blindness; in the other a trace of yellow and blue sensation persisted.

In conclusion, a fourth kind of achromatopsia is that seen at the retinal periphery in deuteranopes, where the distribution of luminosity in the spectrum is the same as that of normal people, which—on Schenck's theory—is due to the fact that all the receptors are associated with all the stimulators. There are cases of congenital and pathological achromatopsia in which the peripheral colour-blindness of deuteranopes and normals extends over the whole retina. Congenital cases have been described by Becker and by Piper: clinical cases by Schöler and Uthoff, Siemerling and König, and Pergens.

Schenck's theory is an ingenious and very complicated hypothesis to account for all the functions of the retina, particularly the different varieties of partial or total colour-blindness—which could not be interpreted by any of the previous theories.

It is undoubtedly a marked advance on those of his predecessors, of which it is to a large extent the elaboration.

That it can account for all the facts may, however, be doubted. If we accept the two phases of the panchromatisation of the primitive visual substance, in the first of which the white substance splits into blue and yellow, in the second the yellow into red and green, it is not easy to understand why the visual field for yellow is slightly more extensive than that for blue, and the visual field for red more extensive than that for green. According to Schenck's theory the yellow field ought to coincide with the blue field, and the red with the green field, because the substances which subserve the two pairs of complementary colours are, on this theory, produced simultaneously. The same difficulty (as Carincione rightly pointed out) is encountered in explaining why, in progressive atrophy of the optic nerve, sensation to green entirely disappears, at a time when that to red still persists, though only to a very limited extent.

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CHAPTER VIII

OCULAR MOVEMENTS AND VISUAL PERCEPTIONS

CONTENTS.—1. Articulation of eye-ball in its socket; its external muscles; its movements and possible positions. 2. Isolated and associated movements of its muscles. 3. The innervation and co-ordination of the eye-movements. 4. Simple binocular vision and the horopter. 5. Diplopia. 6. Conflict between the visual images of both eyes and the phenomena of binocular contrast. 7. Spatial perception in monocular and binocular vision. 8. Stereoscopic binocular vision; the stereoscope. 9. Psychophysical processes on which visual perceptions and representations depend; relativity of our judgments of size, distance and form; optical illusions and visual hallucinations. 10. Protective apparatus of the eye. 11. Origin of the aqueous humour. Bibliography.

IN the last chapter we discussed the simplest and most elementary characteristics of Vision, including the sensations of light and colour produced by stimulation of the elements of the retina, apart from the manifold and varied sensations that are simultaneously aroused at the different points of the retinal surface.

On this complex of sensations depend our visual perceptions, that is, the knowledge we acquire of external objects through the central organs of vision. The impression commonly made upon us by the visible world is not that of a multitude of separate and independent elementary sensations, but rather of a greater or less number of compound sensations, which we project outwards by means of psychical processes of synthesis and association, and transform into perceptions of the objects, judging of their brightness and colour, their form, size, and distance, and the nature and velocity of their movements.

Till now, moreover, we have only been considering *uniocular* vision, whereas our ordinary sight is *binocular*, and is dependent on the great mobility of the eye-balls, and the associated and variously co-ordinated activity of their external muscles. In uniocular vision objects are viewed almost entirely in one plane. Their distance can only be appreciated by the effort of accommodation, which does not come into play for long distances. Uniocular vision is therefore imperfect. Binocular vision gives us the following advantages:

(*a*) Greater extension of the visual field;

(*b*) More perfect inspection of space, since we can look at an object from two fixed points, which makes stereoscopic or tri-dimensional vision possible;

(*c*) Facilitation and greater accuracy in judging the distance and real size of objects;

(*d*) Possibility of correcting congenital and acquired defects in one eye by means of the other.

Before commencing the study of visual perceptions and judgments we must therefore examine the movements of the eye-

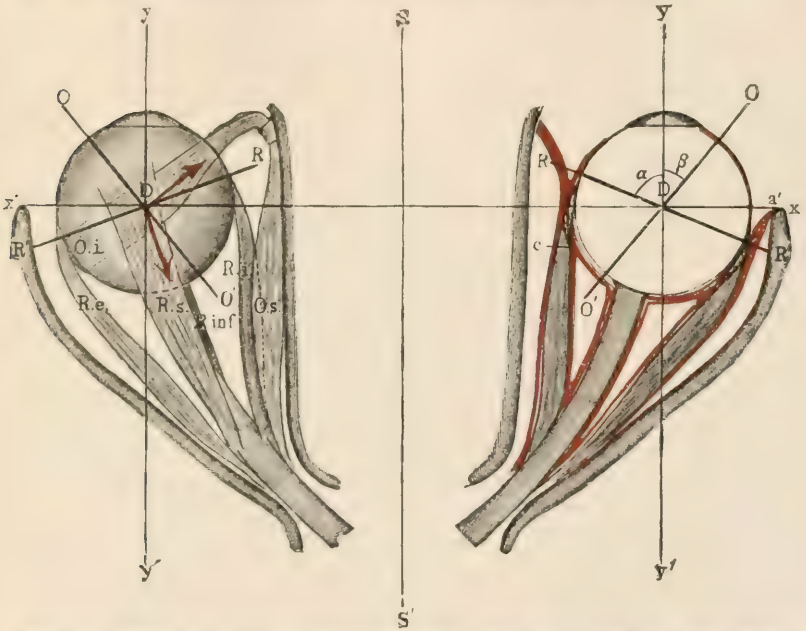


FIG. 182.—Diagram of the motor apparatus of the eye. Natural size. (Motais.) The left figure shows more particularly the attachments and course of the muscles; the right, the relations of Tenon's capsule. Explanation of letters in text.

ball produced by its external muscles, since this is essential to the right understanding of the phenomena of binocular vision.

I. The eye-ball is contained in the orbital cavity framed by bony walls, which is in the shape of a quadrangular pyramid with the point tilted backwards. The space comprised between the walls of the cavity and the eye-ball is occupied by loose adipose tissue, by the external eye-muscles, and by the lachrymal glands—all of which are provided with vessels and nerves.

The nasal walls of the orbit are almost parallel to each other (Fig. 182), while the temporal walls diverge from behind forwards at about 24 -30° from the axes of the two cavities. The anterior margins of the orbital cavity are curved inwards above and at

the sides; the lateral border recedes backward, so that the temporal side of the front half of the bulb is practically uncovered. In eyes of normal size the line that joins the two outer edges of the orbit passes approximately through the rotation-centres of both eyes (line *x'x* of figure).

The hollow space which contains the eyeball is formed behind by Tenon's capsule and the peribulbar and retrobulbar cushions of fat, in front by the inner surface of the lids and the conjunctival sac. Attached only to the optic nerve, like a fruit to its stalk, the eye can be rotated in its cavity by the recti muscles in four directions, corresponding to the four sides of the orbit: but owing to the incompressibility of the solid and liquid tissues which surround it, it is but little displaced.

Tenon's capsule, according to Motais (1887), is an aponeurotic membrane which takes origin in the periosteum of the optic foramen and is attached in front to the margin of the orbit: it provides a sheath for the external ocular muscles, the optic nerve and the sclerotic (Fig. 182, right). The inner surface of the capsule is attached to the sclerotic only by delicate bundles of connective tissue, and is, for the most part, separated from it by a wide lymphatic space, so that when the eye moves it serves as a synovial capsule.

The sheaths which the capsule provides for the recti muscles are thicker, and adhere more closely to the substance of the muscles near their tendinous attachments to the eyeball: ligamentous expansions from their outer sides are attached to the margin of the orbit (*aa'* of figure): at the inner sides they are continuous with a semi-lunar thickening of the capsule, the ligamentum capsulare (*c* of figure). These elastic and distensible bands are of importance, since by fixing the eyeball anteriorly they limit the effect of traction of the muscles and act as regulators of the movements of the eye when its muscles contract (Motais). After cutting one of the moderator ligaments the eyeball can make wider excursions to the corresponding side with less effort (Merkel).

The muscles that effect the movements of the eye are attached in front to the equator of the eyeball, like the bridle to a horse's head, and behind to the bony walls of the optic foramen. There are four recti and two obliqui muscles. The anterior tendinous attachments of the recti muscles are often arranged spirally, according to Tillaux, since the rectus internus is inserted about 5 mm. from the edge of the cornea, the rectus inferior 6, the rectus externus 7, and the rectus superior 8 mm. The internal rectus is the broadest and strongest, the superior the smallest and weakest. The superior oblique or trochlear muscle takes origin from the inner part of the optic foramen, runs along the inner wall of the orbit, and passes as a small round tendon through a

fibro-cartilaginous ring (trochlea) attached to the fovea trochlearis of the frontal bone; it then bends outward and backward, and is fixed below the inner margin of the superior rectus to the equator of the eyeball. The inferior oblique arises from the inner wall of the orbit just below the fossa sacci lacrimalis; it runs outward, bends back and up between the inferior and external recti, and is inserted on the outer and lower part of the eyeball, opposite to and parallel with the insertion of the superior oblique, as a flattened muscle without a tendon. To realise how these muscles produce the ocular movements it is necessary to assume that all the movements take place round a given fixed point, known as the *centre of rotation of the eyeball.*

The position of the centre of rotation (*Drehpunkt*) varies somewhat with the form of the eye. Junge, Donders, and Doijer showed that in emmetropic eyes it lies 13·54 mm. behind the summit of the cornea, in hypermetropic 12·32 mm., in myopic eyes 15·86 mm. The centre of rotation of the average emmetropic eye lies about 1·3 mm. behind the middle point of the eye.

The three principal axes of the eye pass through its centre of rotation (*D*): the sagittal axis (*yy'*) coincides with the line of vision; the transverse axis (*xx'*) coincides with a line that unites the outer or temporal edges of the orbit; the vertical axis (not shown in figure) passes through the eye perpendicular to the horizontal and transverse axes. These three axes constitute a system of co-ordinates which intersect at a right angle in the centre of rotation.

Three planes are also spoken of in the eye, their position being always relative to the two axes: the *horizontal* plane, corresponding to the sagittal and transverse axes, divides the eye into upper and lower halves; the *vertical* plane, corresponding to the vertical and horizontal axes, divides the eye into inner and outer halves; the *equatorial* plane, corresponding to the vertical and transverse axes, divides the eye into posterior and anterior halves. The horizontal and vertical planes cut the fovea centralis of the retina, and divide it into four quadrants.

Helmholtz gave the name of *line of sight* or *vision* (*Blicklinie*) to the vertical axis which unites the centre of rotation of the eye to the fixation point; the *plane of sight* or *visual plane* (*Blickebene*) passes through the visual lines of both eyes, and is halved by the medial sagittal plane of the body (*SS'* of Fig. 183).

The *fixation point* (*Blickpunkt*) of the eye can be raised or lowered, or turned from side to side. The field which can thus be covered by the eye while the head remains motionless is the *field of vision* (*Blickfeld*); it corresponds to a portion of a spherical surface, with the rotation point of the eye as its centre.

Given the primary position of the eyes (lines of sight parallel, and plane of sight horizontal), the degree to which the visual

plane is raised or lowered is determined by the angle formed with the visual plane of the primary position; the lateral deviation of the visual axis is determined by the angle formed with the median line of the plane of vision. The first is the angle of elevation or depression: the second, the angle of lateral deviation (adduction or abduction), which brings the eye into the secondary position.

The eyeball can also execute more complicated movements, in which the lines of sight converge or diverge, and are at the same time directed upwards or downwards, by simultaneous rotation round the vertical and the transverse axes. These oblique movements bring the eye into the tertiary positions. The eyeball can also rotate round the visual axis by a wheel movement. This rotary movement is always associated with a tertiary position, and never occurs independently owing to the co-ordinated innervation of the eye-muscles.

II. The most accurate measurements which it is possible to take of the points of origin and attachment of the several muscles of the eye, relatively to the co-ordinates described above, show that the three pairs of muscles are not perfectly antagonistic, since the axis of rotation by the superior rectus does not coincide with that by the inferior rectus, nor that by the internal rectus with that by the external rectus, nor that by the superior oblique with that by the inferior oblique. But the differences in the angle made by the axes of rotation of each pair of muscles with the co-ordinates are insignificant; it is only the angle formed by the two axes of rotation of the obliques with the sagittal axis that amounts to the perceptible value of 6°. These differences may therefore, for simplicity, be neglected, and we may assume with Volkmann that each pair of muscles moves the eyeball by antagonistic action to the others round a common axis.

To determine the action of each pair of muscles it is necessary to ascertain the plane of traction in which they work, and the common axis of the rotation round which they move the eyeball in antagonism. The former is easily discovered if we imagine a plane passing through the points of origin and attachment of the muscles, and the centre of rotation of the eye; the latter is represented by the perpendiculars dropped from the centre of rotation upon the plane of traction.

The measurements carried out by Ruete and A. Fick gave the following results:—

(*a*) The internal and external recti rotate the eye inward (adduction) and outward (abduction). As shown in Fig. 183 their plane of traction coincides with the plane of the page; *QE* shows the traction of the external rectus, *Q′I* that of the internal rectus; the axis of rotation coincides with the vertical axis of the eye, which is perpendicular to the centre of rotation *O*.

(*b*) The superior and inferior recti rotate the eye upward and somewhat inward, or downward and somewhat inward. Their axis of rotation (dotted line *R. sup.—R. inf.*) lies in the horizontal plane of the eye, but forms with the transverse axis (*QQ'*) an angle of about 20°; the direction of traction of both muscles is shown by the line *si*.

(*c*) The inferior and superior obliqui rotate the eye outward and upward, or outward and downward. Their axis of rotation (dotted line *Obl. inf.—Obl. sup.*) also lies in the horizontal plane of the eye, but forms an angle of about 60° with the transverse axis; the direction of traction of the inferior oblique is shown by the line *ab*, that of the superior oblique by the line *cd*.

Ruete, in 1846, so as to imitate the eye-movements effected by the isolated and associated movements of the three pairs of muscles as perfectly as possible, constructed a special model of the two eyeballs with the corresponding muscular attachments, or "*ophthalmotrope*," which was subsequently modified by Wundt, Ludwig, Landolt and others.

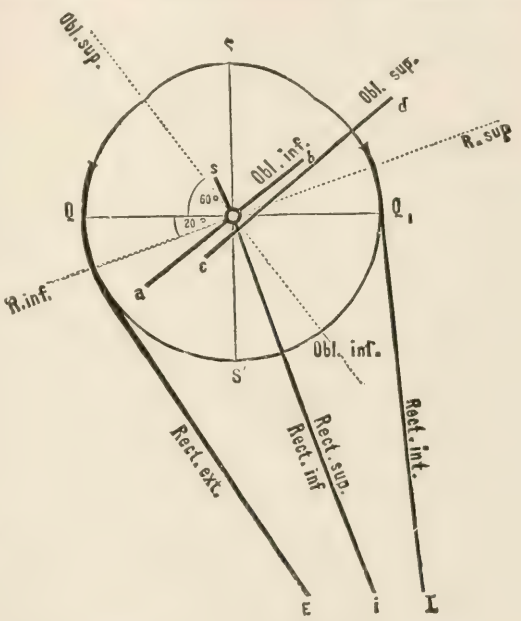


FIG. 183.—Diagram to show axes of rotation of the eyeball, and lines of traction of the external ocular muscles. (Landois.)

With the ophthalmotrope Hering obtained an almost perfect diagram of the form and direction of the movements of the visual axis in the field of vision, when the (left) eyeball is moved by its respective muscles from the primary to the secondary positions (Fig. 184).

When the eyes are at rest, as is always the case in sleep, the muscles are in a position of equilibrium, determined by the differences of their strength and tone. As the internal recti are the strongest, the visual axes of the two eyes converge slightly, and cross at a distance of about 40 cm. in the median line. We must therefore conclude that in the primary position of the eyes, when the visual axes are parallel in distant vision, the two external recti are in a state of moderate contraction.

The eyes are rotated to the right or left from the primary position by contraction of the external rectus of the right and the internal rectus of the left side, and *vice versa*. But to move the eyes up or down, the contraction of the two superior or inferior recti is not sufficient, the associated contraction of the oblique muscles being also required — that of the superior rectus and inferior oblique in raising the eye, of the inferior rectus and superior oblique in lowering it. These two pairs of muscles work

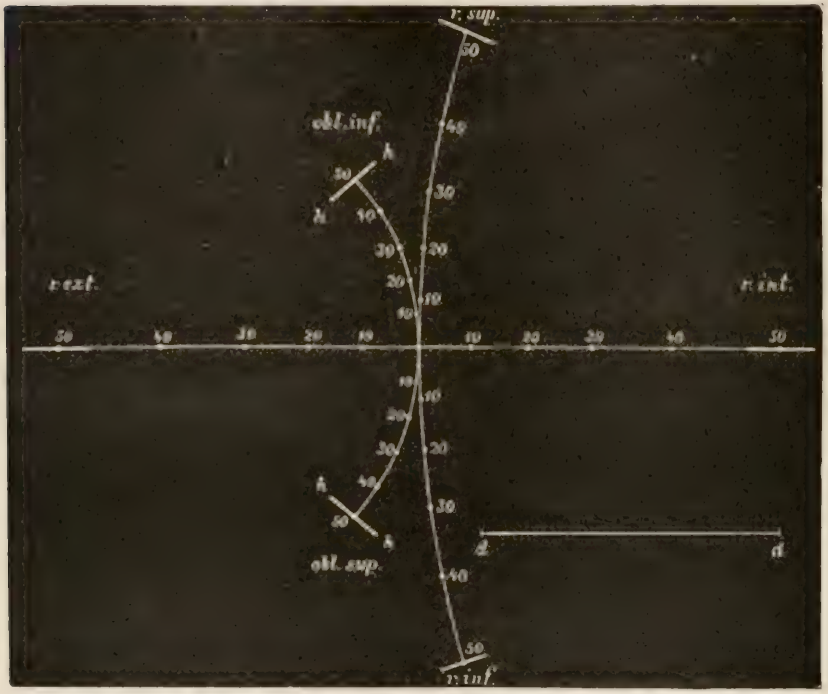


FIG. 184.—Diagram showing the direction of movement when the eyeball is rotated from the primary position by the action of the different muscles. (Hering.) The angles of rotation corresponding to the movements of the visual axes are indicated on the lines in degrees. *dd* represents the distance of the plane of sight (which here corresponds with the plane of the figure) from the centre of rotation of the eye. The position of the horizontal meridian at the end of the movement is indicated by the short heavy line at the extreme ends.

together in turning the eye up or down, but their action is also antagonist since the recti rotate it inwards and the obliqui rotate it outwards; these opposite rotations, however, compensate each other, so that the resultant of the double action is an upward or downward movement of the eye.

The synergic action of two muscles does not suffice for the diagonal or oblique movements which carry the eyeball into the so-called tertiary positions, and three muscles are involved:—

(*a*) For rotation inward and upward, the internal rectus, superior rectus, and inferior oblique;

(*b*) For rotation inward and downward, the internal rectus, inferior rectus, and superior oblique;

(*c*) For rotation outward and upward, the external rectus, inferior rectus, and inferior oblique;

(*d*) For rotation outward and downward, the external rectus, inferior rectus, and superior oblique.

These oblique movements may, as above stated, be associated with a slight degree of rotation or rolling of the eye round the horizontal visual axis.

The recti muscles are stronger than the obliques, but this difference is compensated by the fact that the axes of the latter are more diagonal, and are therefore capable of rotating the eye more vigorously round the visual axis. So that when the superior rectus and inferior oblique, or the inferior rectus and superior oblique, contract to the same strength, and act synergically, the rotatory effect of the obliques is to a large extent eliminated.

It must not be forgotten that this description of the action of one, two, or three muscles in the movements of the eye is only a simplification or diagrammatic representation of the facts, since it assumes a common axis of rotation for each pair of muscles, whereas in reality each muscle has its own axis. Remembering this we must admit with Volkmann that every movement of the eye, even the simplest, requires the synergic and unequal contraction of a number of muscles.

Moreover, the muscular actions which we have enumerated for the production of single movements hold good only when the eye is in the primary position at the outset, because the axis of rotation of each muscle of course changes when it is in any other position. Thus, for example, the contraction of the superior or inferior oblique may suffice alone, with weak or negligible intervention of the superior or inferior rectus, to rotate the eye up and down when it is adducted: when, on the contrary, the eye is abducted, the sole or almost exclusive contraction of the superior or inferior rectus suffices to rotate it upward or downward.

Under normal conditions the movements of both eyes are intimately associated; they move simultaneously. Even when one of them is blind, or when both have been excised, the muscles of both contract in response to impulses of central origin. The range of the movements diminishes somewhat with age. Mobility is more restricted in the vertical than in the horizontal direction, upward than downward.

Under normal conditions, with the head upright, the movements always take place so that the two visual axes lie in the same plane. One eye cannot direct its visual axis higher or lower than the other, nor is it possible for the two axes to diverge

further than to bring them parallel, as in the primary position. When the normal association of the binocular movements is defective, a *squint* (*strabismus*) occurs, and the two visual axes no longer lie in the same plane, nor are they capable of converging upon a single point, nor of becoming a parallel to one another. In *nystagmus*, on the contrary, the normal association of binocular movements is maintained.

The visual axes can be moved in any direction from the primary position without rotation or wheel movement. This is shown by the method of Ruete and Helmholtz, which consists, with the head at rest in the primary position, in fixating two coloured bands in the form of a cross, which are fastened on a wall 1-2 m. away, so as to obtain an after-image. If, after sufficiently long fixation, the eye is moved from the primary to a secondary position (*i.e.* upwards or downwards, to the right or to the left), it will be found that the after-images of the horizontal and vertical parts of the cross remain unchanged, proving that there is no rotation round the visual line. If, on the contrary, the eye is moved from the primary into the tertiary position (as upwards to the right or left, or downwards to the right or left), it is found that the lines of the after-image become oblique (Fig. 185). This effect is not, however, due to the rotation of the eye round the visual line, but simply to the fact that the median plane of the eye, which is vertical in the primary position, becomes oblique when the eye is rotated into a tertiary position.

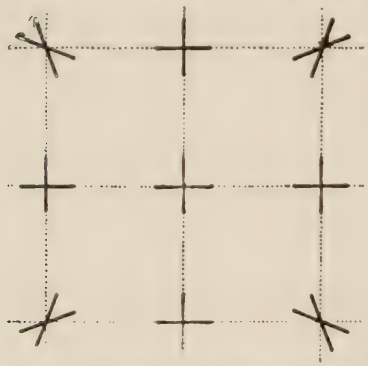


FIG. 185.—Projection of the after-image of a rectangular cross in nine different directions of the visual axis. (Helmholtz.)

In all these cases, therefore, the movements of the eye conform to Listing's law. Whenever in the emmetropic and parallel directed eye the visual axis is moved from the primary into any other position, the movements of the eyeball take place round fixed axes, each of which is at right angles to the plane of the movements of the visual line; and both lie in the same plane, at right angles to the primary position of the line of vision.

Normal binocular movements may be classified in three groups:

(*a*) Movements with the two visual axes *parallel* (long distance vision).

(*b*) Movements when the two visual axes *converge* at a point of the median plane (short distance vision).

(*c*) Movements when the two axes are *convergent* and *non-*

parallel (short distance vision of points situated to the right or left of the median plane).

The latter are accompanied by a sensation of effort. They rarely occur, and are difficult to perform at will. When we attempt to fixate a near object situated laterally (above, below, or in the horizontal plane), we instinctively prefer to turn the head to the right or left rather than the eyes, so as to avoid the sense of effort associated with convergent and lateral movements, particularly with those that bring the eyes into tertiary positions.

It follows that the movements which we actually carry out with our eyes are far less numerous than appears from the theoretical consideration of the action of their muscles. This restriction of the eye-movements depends on the co-ordination of the nerve-centres which innervate the muscles of the eye. It is, as we shall see, of great importance in visual perception, because it produces a closer and more constant relation between the retinal images and the positions of the eyes.

III. We have already seen, in speaking of the central origin and the peripheral distribution of the cranial nerves (Vol. III. vii. p. 411), that the motor nerves of the eye are the third, fourth, and sixth cranial. The first-named (oculomotor), besides innervating the levator palpebrae, the pupillary sphincter, and the ciliary muscle, also supplies all the external muscles of the eye, except the superior oblique which is innervated by the fourth (or trochlear) nerve, and the external rectus innervated by the sixth nerve (or abducens).

These three motor nerves are exceptionally large in comparison with the cross-section of the ocular muscles. The oculomotor has, on an average, a cross-section of 3 sq. mm. and contains 15,000 nerve-fibres (Krause); the abducens has a cross-section of 2 sq. mm. and 3600 fibres (Tergust); the trochlear of 0·4 sq. mm. and 2150 fibres (Merkel).

The third and fourth cranial nerves arise from a common nucleus of grey matter 5-6 mm. in length, which lies below the aqueduct of Sylvius at the level of the anterior, and of the most anterior part of the posterior corpora quadrigemina; the sixth nerve springs from a small nucleus, situated about the middle of the sinus rhomboidalis, a little above the striae acusticae, within the genu of the facial nerve (Fig. 204, Vol. III.).

Although anatomically undivided, the nucleus of the third and fourth nerves falls, according to the clinical studies of many authors, particularly the interesting experiments of Bernheimer (1899–1902) upon the monkey, into a number of small nuclei, which overlap more or less, and are connected with separate eye-muscles. From above caudalwards these are the nuclei for the levator palpebrae, superior rectus, internal rectus, inferior oblique, inferior rectus, and finally the superior oblique (nucleus of the

fourth nerves). According to Bernheimer's diagram (Fig. 186) the nucleus of the levator palpebrae and that of the superior rectus are connected with the corresponding muscles by direct or homolateral fibres; the nucleus for the internal rectus and that for the inferior oblique send to their corresponding muscles both direct and crossed fibres; while the fibres of the nucleus of the inferior rectus—and according to Panigrossi of the superior oblique as well—all cross. The nucleus of the sixth or abducens nerve, which is distinct from the nuclei of the third and fourth nerves, sends out, according to Bergmann's investigations, only direct fibres.

Intimately connected with the mass of the bilateral nuclei of the third and fourth nerves (which Bernheimer terms the *principal nuclei*) are three other small nuclei (which he calls *accessory*), one unpaired, median, with large cells (*M*), the other two symmetrical, with small cells (*mm*). The motor fibres that run out from the accessory nuclei are slender and myelinate late; they run medialwards, and unite with the oculomotor without decussation. According to Bernheimer, the principal nuclei innervate the external ocular muscles, and the accessory nuclei the internal muscles, *i.e.* the sphincter of the iris and the ciliary muscle. Both the direct and the crossed fibres of the roots remain separate within the mid-brain, and only unite in the trunk of the oculomotor nerve shortly before leaving it.

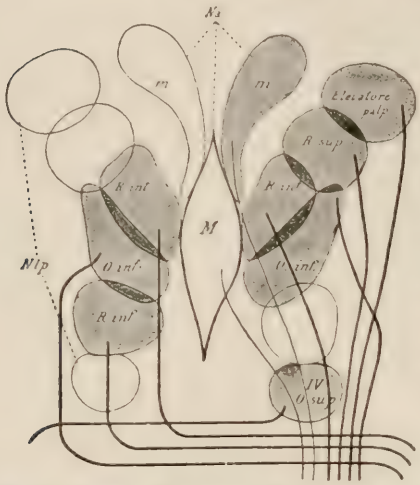


FIG. 186.—Diagram of the nuclei of the oculomotor nerves. (Partly after Bernheimer.) *Nlp*, lateral principal nuclei; *Na*, mesial accessory nuclei. Other explanations in text.

Bernheimer determined the localisation of the different nuclei that innervate the external and internal ocular muscles in monkeys with Nissl's method of studying the central lesions that occur after the removal of the muscles (1897), as well as by the isolated electrical stimulation of the different parts of the nucleus (1899).

The anatomical foundation of the bilateral association and co-ordination of the eye-movements depends on the reciprocal relations of the different nuclei of origin, as well as their relations with the optic nerve and the cerebral cortex.

The nuclei of origin of the motor nerves to the eye are

connected both by transverse fibres which unite the nuclei of the two sides, and by ascending and descending longitudinal fibres, contained in the so-called *dorsal longitudinal bundle*, which connect the nuclei at different levels.

Bernheimer noted that in monkeys a median incision through the region of the oculomotor nuclei disturbed the synergy of binocular movement—each eye moved irregularly, and independently of the other eye; the cells of each nucleus therefore only innervate the homolateral eye-muscles.

Different views as to the direct and indirect connections of the optic nerve with the motor nuclei of the internal or external ocular muscles have been enunciated by Stilling, Meynert, Kölliker, Bechterew and others. Bernheimer, after enucleating one eye, or dividing one of the optic nerves in the monkey, was able, by Marchi's method, to demonstrate a bundle of fibres which runs from the optic nerve to the anterior corpora quadrigemina, and thence to the oral end of the lateral medial nucleus. As the degenerated and non-degenerated fibres can be observed in approximately equal numbers on both sides, this gives anatomical proof that about half the fibres of the optic nerve decussate in the chiasma, and that both the crossed and the direct fibres run through the anterior quadrigemina towards the oculomotor nuclei.

The relations of the oculomotor nuclei with the cortex cerebri were ascertained by cortical faradisation. Ferrier, Luciani and Tamburini, Knoll, Horsley and Schäfer, and Risien Russell found that stimulation of the gyrus angularis in the monkey produced rotation of the eyeballs towards the opposite side, and also upward and downward; but if the stimulation is too strong these eye-movements are associated with other more extensive and diffuse movements of the face and head. With very weak induced currents Bernheimer (1899) found that the reactions were confined sharply to the eye-muscles. Stimulation of the right angular gyrus—particularly of the median thirds of its two limbs—produced synergic movements of both eyes to the left, or to the left and upward or downward, and *vice versa*. Removal of the cortex of the angular gyrus on one side is followed by obvious paresis of the eye-movements towards the opposite side, which disappears almost entirely in the second week after the operation.

After Adamük's experiments on electrical stimulation of the anterior quadrigemina it was almost universally admitted that these bodies represent the reflex centre for eye-movements. Bernheimer, however, proved that monkeys after uni- or bi-lateral destruction of these parts are still able to carry out all normal movements of the eyes. Topolanski found the same in rabbits. Bernheimer also showed that after this lesion excitation of one

or other gyrus angularis still produces synergic movements of the eyes. On the other hand, these cannot be obtained when the brain-stem has been divided between the aqueduct and the region of the oculomotor nuclei, showing that the fibres which unite these nuclei with the gyrus angularis undergo complete decussation in the median line below the Sylvian aqueduct.

Fig. 187, published by Bernheimer (1902), is a diagram of the paths which subserve the associated lateral or convergent

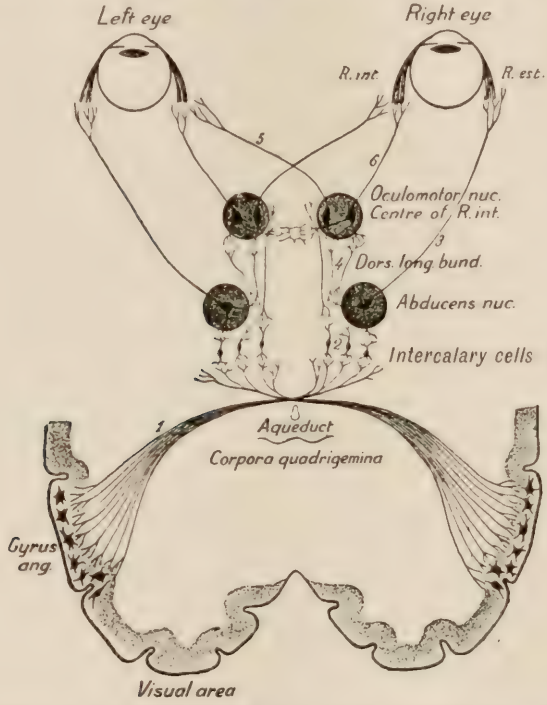


FIG. 187.—Diagram of nerve paths concerned in lateral and convergent movements of both eyes. (Bernheimer.)

movements of the eyes. When both eyes are voluntarily turned to the *right*, the motor impulse starts from the region of the *left* angular gyrus, travels along paths 1, 2, 3, and produces contraction of the external rectus of the *right* eye, simultaneously travelling along paths 1, 2, 4, 5 contraction of the internal rectus of the *left* eye. If the eyes converge voluntarily, the impulse starting from the angular gyrus of one or both hemispheres travels along paths 1, 2, 4, 5 and 1, 2, 4, 6, and produces contraction of the internal recti of both eyes.

It is easy to understand that, after unilateral destruction of the gyrus angularis or of paths 1, there must be conjugate

deviation of both eyes towards the side of the lesion owing to the predominance of the non-paralysed antagonist muscles; convergence, on the contrary, is unaffected, because the angular gyrus and the paths from one hemisphere to the internal recti of both eyes are intact. The conjugate deviation may be compensated in time; but, if the lesion is sufficiently extensive and complete, the inability to turn the eyes towards the side opposite that of the lesion persists.

Voluntary cortical impulses may proceed directly from the gyrus angularis, or be transmitted indirectly to the gyrus angularis from the visual area or other regions of the cortex (frontal lobe) by the association fibres which unite the different parts of the cerebral cortex into a single organ.

Involuntary reflex movements of the eyes are excited principally through the optic nerves, and, according to Bernheimer, the impulses reach the cortical centres directly, without interposition of the grey matter of the anterior corpora quadrigemina, as was formerly assumed by Meynert and Kölliker.

The nature of the anatomical and physiological basis of the exceedingly delicate, rapid, and certain co-ordination of the eye-movements which subserve *directive adaptation* is a very difficult problem which has not yet been adequately solved. It may be stated generally that it does not depend exclusively upon a *sensation of innervation* preceding the volitional impulse that changes the direction of the visual axes, as assumed by Meynert, Bain, Helmholtz, and Wundt; nor upon the peripheral kinaesthetic sensations which accompany the contraction of the eye-muscles, as maintained by James and Münsterberg; but it is also due to the changes in position of the objects in the field of vision which accompany the displacements of the visual axis. According to Helmholtz we constantly use this displacement of objects as a control of the proper relation between the volitional impulses and their effects. It is obviously of greater importance in consciousness than the obscure kinaesthetic sensations of innervation which precede or accompany the eye-movements, and is in itself adequate to account for the rapidity of *directive adaptation* in the external muscular system, which is associated and co-ordinated with the accommodation and convergence of the internal muscles of the eyes.

IV. Owing to this central association and the co-ordination of their movements, the two eyes constitute a *single binocular instrument*, which Hering termed the "double eye." The two eyes are habitually in such positions that the points towards which the two visual axes are directed, and which form images upon the two foveae centrales of the retina, induce *single vision*—that is, the central fusion of the two images into one.

The fundamental conception underlying *single vision* with

the two eyes is that the visual axes shall constantly intersect at the fixation point, *i.e.* they must always remain in the same plane, and converge, in fixing near objects, or remain parallel, in fixing distant objects. When this does not occur there is *squint* or *strabismus*.

Since binocular vision occurs not only when both eyes are in symmetrical positions, that is, when we focus objects lying in the same plane, but also when they are asymmetrical, we must conclude with Hering that both the vertical and the lateral movements of the two eyes are equal, it being an indispensable

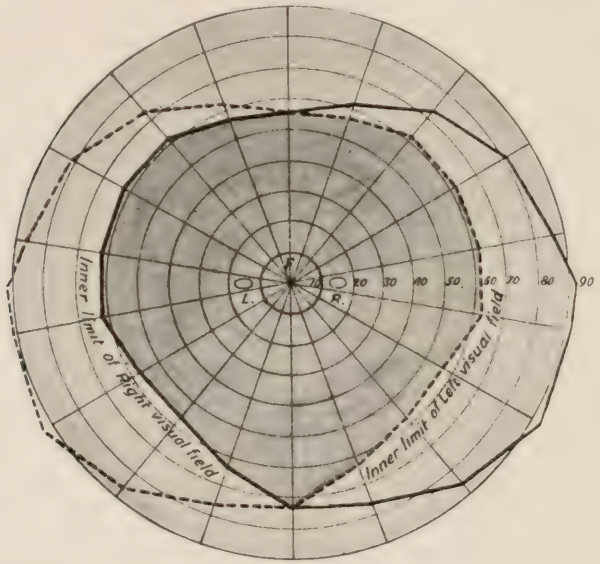


FIG. 188.—Binocular field of vision. (Sulzer.) *F*. Common fixation point for both uniocular fields; *L*, blind spot of left visual field; *R*, blind spot of right visual field. The continuous line limits the right, the broken line the left visual field; the area of the binocular visual field is shaded grey.

condition that the two visual axes shall lie in the same plane and constantly converge on the common point in space. This perfect co-ordination of the two eyes is brought about, as we have seen, by special organisation of the cerebral centres; on this depends the *directive adaptation*, *i.e.* the perfect compensation and correlation of the motor innervation of the homonymous and antagonist muscles.

It is also necessary for binocular vision that the point of convergence of the two visual axes shall fall within the binocular field of vision. This results from incomplete superposition of the two uniocular visual fields, for (as shown by Fig. 188) the outer part of the visual field of the right eye, corresponding with the

nasal side of the right retina, extends much farther to the right than the inner part of the visual field of the left eye, corresponding with the temporal side of the left retina. Similarly, the outer limit of the visual field of the left eye extends farther to the left than the inner limit of the visual field of the right eye. The field common to both eyes, on convergence of the two visual axes at the point *F*, is represented by the shaded area, and in this only is there vision with the "double eye." In many animals the position of the eyes lies so much to the side that the two fields of vision do not intersect, and consequently they have only uniocular vision.

The blind spot of the left visual field falls, in the binocular field of vision, on a seeing part of the right visual field, and *vice versa*, so that there is no physiological scotoma when we employ binocular vision.

In order to have single vision in the binocular visual field it is necessary for the images of the object to fall on certain points of the two retinae, which are known as *corresponding* or *identical points*. When this fundamental condition is not fulfilled, *i.e.* when the images of the object fall on disparate non-corresponding points of the two retinae, *diplopia* or *double vision* of the object results.

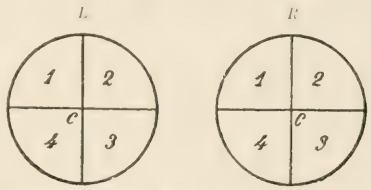


FIG. 189.—Diagram of identical or corresponding points in the two retinae. *L*, left eye; *R*, right eye; *c*, centre of fovea.

What are the corresponding points, *i.e.* the points in the two retinae, which, when excited simultaneously, produce single vision—that is, vision of the image in the same part of the binocular field of vision?

It is plain that the centres of the two foveae are identical points, because on focussing any point with the double eye both visual axes converge upon it. If we picture the two retinae as perfect sections of spheres the poles of which correspond with the centres of the foveae, and divide each retina into four parts by lines in the vertical and horizontal meridians intersecting at a right angle at the centre of each fovea (Fig. 189), we may consider that not only the poles (*c*) but also all corresponding points in the four quadrants (1, 2, 3, 4) of the two retinae would be identical if the two retinae were superposed. Or better, we may say, with Johannes Müller, that not only the central points of the two foveae, but all points that are equidistant in the same meridian from the centre of the foveae, are identical.

This geometrical definition of the corresponding points cannot, however, be regarded as exact, because the four segments of the two retinae are not fully congruent. Later investigation with more perfect methods showed a slight "physiological incongru-

ence" of the two retinae, into which we need not enter as it has little practical importance.

Passing from the centre to the periphery of the retina, the determination of corresponding points becomes increasingly uncertain, especially in the lateral direction (Mandelstamm and Schöler).

The simplest case of binocular vision is that in which the two eyes are in the primary position, with the two visual axes parallel and in a horizontal plane. On fixating a distant point on the horizon or a star in the sky we see singly not only the point or star which form images in the centre of the two foveae (direct vision), but also the surrounding points or stars which form images more or less removed from the centre of the foveae (indirect vision). Johannes Müller gave the name of *horopter* to the geometrical figure which results from the spatial points that are seen singly with the double eye, and therefore form images on corresponding points of the two retinae.

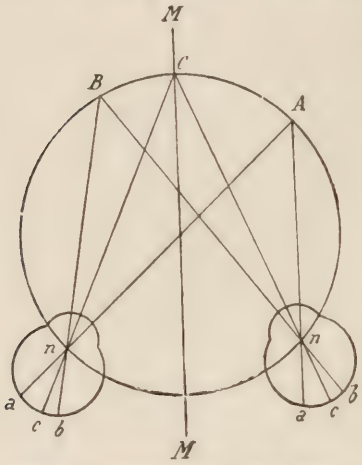


FIG. 190.—Horopter circle. (Joh. Muller.)

All spatial points not included in the figure of the horopter appear double when we direct our attention upon them, the more so in proportion as they are removed from the horopter, because their images fall on disparate points of the retina.

Each position of the binocular apparatus has its corresponding horopter figure.

(*a*) When the eyes are in the primary position, the horopter would be represented by a vertical plane situated at infinite distance, if the vertical axes of the two retinae were exactly parallel. Actually, however, this is not the case: if the visual axes of the eyes are set for vision at a long distance, the vertical axes converge somewhat below, so that, in the erect position of the head, they intersect at about the level of the plane of the feet (Helmholtz). It follows that not only the points of the horizon, but also those on the plane on which we stand, are seen in single vision—an obvious advantage to vision as a whole.

(*b*) When the eyes are in a secondary position, *i.e.* when the visual axes converge and lie in the horizontal plane, the horopter is formed like a circle passing through the nodal points of both eyes and the point of convergence of both visual axes (Vieth and Joh. Müller). In Fig. 190, *C* is the convergence point of the two visual axes along the median plane *MM*; *cc* are the central

points of the foveae; *aa* and *bb* are corresponding points of the two eyes, because they are equidistant from *c* and lie in the same meridians. The circle passing through the nodal points *nn* and *C* represents the horopter, because each of its points forms an image on identical points of the two retinae; point *A* at *aa*, point *B* at *bb*. The horopter has the same form in asymmetrical secondary positions of the eyes, *i.e.* when the point fixated lies outside the median plane. If in Fig. 190 the point fixed is not *C* but *A*, and the lines *Aa* fall on the central points of the foveae, then points *C* and *B* will fall on corresponding points of the retina, and points *A*, *B*, *C* and all others along the line of the circle form the horopter.

(*c*) When the eyes are in an asymmetrical tertiary position (which, as we have seen, is very rarely the case), the horopter is represented in space by a complex curve of double curvature which passes through the nodal points of both eyes (Helmholtz).

V. We have seen that when the images fall on the two retinae of the double eye at disparate or non-corresponding points there is *double vision*. This is the more obvious the greater the incongruence or the distance between the points on which the two images fall from those at which they should form a single image. *Homonymous* and *crossed double images* must be distinguished.

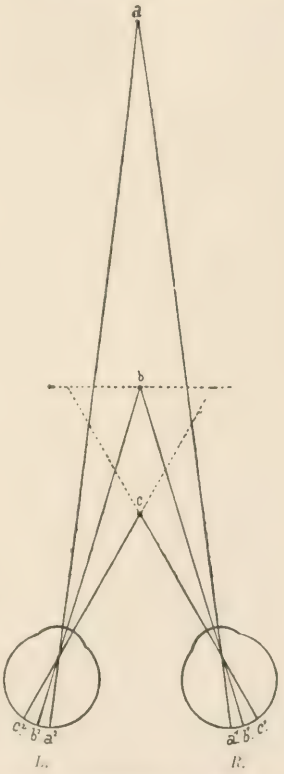


FIG. 191.—Geometrical construction to show the production of homolateral and crossed images.

In Fig. 191 *a*, *b*, *c* represent three points in the median plane of the double eye (*L.*, *R.*). On fixating point *b*, a single, clear image is formed in the two foveae b^1, b^2, while at the same time points *a* and *c* form double images at non-corresponding points a^1 a^2, c^1 c^2. As the double eye is not focussed to the distances *a* and *c*, the double images appear blurred; as point *a* is more distant and point *c* nearer than the fixation point *b*, the double images of the former appear smaller and those of the latter larger than *b*. The two images of *a* are homonymous; that on the right disappears on closing the right eye, and that on the left on closing the left eye. The two images of *c*, on the contrary, are crossed; that on the right vanishes on closing the left eye, and that on the left on closing the right eye. The place to which we refer the double

images of *a* and *c* is not the transverse plane that passes through the fixation point *b*, as was formerly supposed; but we see them at their true distances, *i.e.* in transverse planes, through the points *a* and *c* (Helmholtz, Hering).

Double vision (*physiological diplopia*) occurs not only for the points lying along the median plane, farther from or nearer to the fixation point (Fig. 191), but also for all other points lying beyond the median plane which are not along the horopter-line that corresponds to the position of the double eye. In the latter case, however, the diplopia is less clear and obvious, because the images fall at more eccentric regions of the retina. Generally speaking, it may be said that the double images of objects in space are sharper when they fall on more central regions, increasingly blurred and indistinct as they fall on more peripheral regions, of the two retinae.

It is a fact of common observation that with the double eye we usually perceive only single images in the binocular field of vision, and merely become aware of physiological diplopia under quite special conditions, although the points in space corresponding to the horopter which form images at identical points of the retina are comparatively few in comparison with the countless spatial objects which form images at non-identical points. Several facts can be cited in explanation of this apparently paradoxical phenomenon.

(*a*) We always see the objects singly which we fixate directly and which form images in the central foveae; this is regulated by the three adaptive systems of convergence, accommodation, and pupillary reaction.

(*b*) The objects that we see singly excite the corresponding points of the retinae, with double energy, and thus produce a more intense impression, as if they were viewed through a single median cyclopic eye, whereas the images from two disparate points are blurred and separated.

(*c*) The images formed at identical points of the retinae have an identical 'local sign' of recognition, with which they are intimately associated in consciousness.

(*d*) We fix our attention upon the objects seen single because they form sharp, distinct, and perfect images; while we neglect the objects seen double because they are blurred and indistinct, and readily disappear on moving the eyes.

If we focus an object lying in the binocular field of vision, and displace one of the eyes slightly with the finger, so that the two visual axes can no longer converge on it, the visual field of the eye that is compressed is also displaced, and all objects, including that fixated, appear double. Theoretically this binocular diplopia should be permanent in every case of strabismus, but ophthalmological experience shows that this is not so actually. In cases of

paralytic squint diplopia is the most disturbing symptom to the patient; in *concomitant squint*, on the contrary, the patients do not generally complain of diplopia, either because they are accustomed to neglect the image in the squinting eye, or because the disparate points at which the images in this eye are formed have acquired the property of the fovea of the other eye, so that the two images are superposed in consciousness.

VI. Another interesting phenomenon of binocular vision is that known as the struggle between the visual fields of the two eyes. The simplest case in which this occurs is when we look at a white surface through lenses of differently coloured glass; it is difficult to see the hue resulting from the physical mixture of the two colours; usually there is a successive perception of one or the other colour over the whole field, or one colour prevails in one part of the field and the other colour in the other part, according as the sensation in one or the other eye prevails in all or certain parts of the two retinae. If the observation is prolonged the retinal sensibility to colour becomes blunted, chromatic perception is less unstable and variable, but also more indefinite and dimmed, so that it approximates to grey.

These effects are even better seen when, instead of lenses with different coloured glasses, two differently coloured fields are inspected in a mirror or prism stereoscope.

It is a moot point whether during the alternating predominance of one or the other colour-sensation there is any true binocular mixture of the two colours. Dove, Brücke, Ludwig, Panum, and Hering claim to have observed this mixture; on looking, for instance, with one eye at yellow and with the other at blue, they occasionally saw blue-green. The author has observed the same effect. H. Meyer, Volkmann, Funke, and Helmholtz, on the contrary, never succeeded in obtaining a true binocular colour-mixture. This is probably due to individual idiosyncrasy, and perhaps—as Hering suggests—different observers may interpret the mixture of the two colours with which they are experimenting differently.

If instead of two fields of different colours two discs, one white and the other black, are viewed binocularly, a sensation is obtained of shimmering grey, now darker and now lighter, with a peculiar lustre, which cannot be detected on gazing at either of the discs alone with one or both eyes. The brightness of objects depends essentially on the fact that no point of a shining surface can appear equally bright to both eyes, because it does not reflect the same amount of light in all the different directions. Silk, for instance, shines because each thread reflects the light differently in different directions and the mass of its constituent threads does not present a smooth and homogeneous surface. The lustre in binocular vision of black and white depends on the fact that the elementary

sensations of light and dark are continuously oscillating at each point of the two retinae, as the action now of one eye and now of the other predominates. For the same reason the two photographic images taken for the stereoscope reproduce the natural lustre of objects. In fact, if the two photographs are closely examined, it will be seen that the light parts of the one correspond with the shaded parts of the other, and *vice versa*. Lustre, therefore, results from the rivalry of the sensations of light and dark in both eyes.

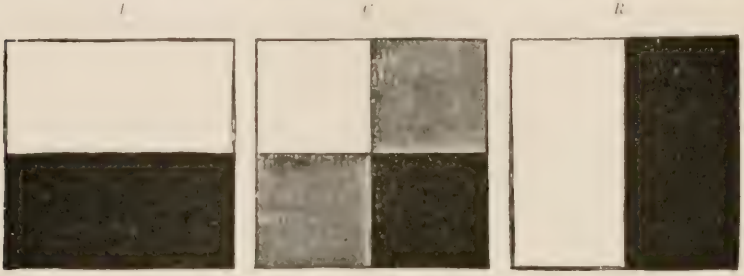


FIG. 192.—Binocular rivalry of contours. (Hering.)

The struggle in the visual fields of the two eyes is even plainer when instead of two surfaces differently coloured, or one white and one black, each eye is confronted with a white and black or bi-coloured surface with sharp outlines, which are not superposed. On looking with a mirror stereoscope at the two lateral, half-white, half-black squares (*L*, *R*) of Fig. 192 they are

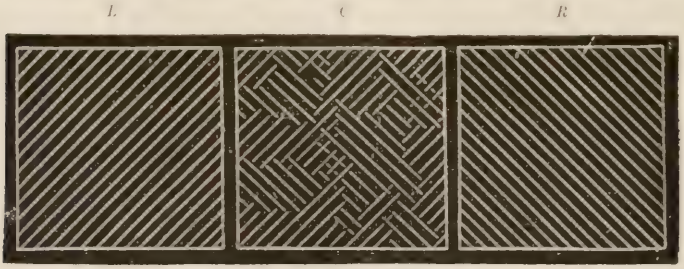


FIG. 193.—Binocular rivalry. (Hering.)

superposed in vision, and the central square *C* appears subdivided into four, one black, one white, and two grey squares of varying luminosity, separated by brighter and darker outlines according as these bound a black or a white square (conflict of outlines).

On superposing the two lateral squares (*L*, *R*, Fig. 193), on the black ground of which oblique and parallel white lines are drawn in opposite directions, the rivalry between the two eyes is evident in gazing at the central square *C*, in which the image of *L* or *R* alternates rapidly in different parts. The predominance

of one or the other image over the whole or certain parts of the binocular field is, according to H. Meyer, Helmholtz, and Fechner, due to oscillations of the attention, which is automatically concentrated on the content of first one and then the other of the visual fields. Panum, on the contrary, gives a physiological explanation of the phenomenon, and refers it to the conflict of outlines. In his opinion the contours or limits between white and black excite the retina more forcibly than the evenly illuminated surfaces, and produce an irregular rhythm of excitation in the cerebral centres.

A further series of effects, studied particularly by Fechner (1860), and more in detail later on by Brücke, Meyer, Panum, and Helmholtz, are known as the phenomena of *binocular contrast.* On closing one eye, and looking at a coloured surface for a few seconds with the other, and then gazing with both eyes at a black card with a vertical white band down the middle, so that two half-images of this band result (physiological diplopia), it is found that the half-image of the fatigued eye shows the complementary colour of the inducing tint (negative secondary half-image), while the half-image of the resting eye shows the contrast-colour (though possibly faded), that is, the same colour that has acted on the other eye (positive secondary half-image). If, for example, the right eye is fatigued with red, the half-image of the white band seen with this eye appears greenish on a black ground, while the half-image of the band seen with the left eye is pink. This difference between the half-images is not due to the fact that they are formed at non-corresponding points of the retinae, because Helmholtz noted the same effect of *binocular contrast,* when the white band on the black ground is fixated so that its image falls on the fovea of the rested or of the fatigued eye, *i.e.* on identical points of the two retinae.

Fechner attempted to explain the phenomena of binocular contrast as the after-effects of the excitation of both retinae; Helmholtz, on the other hand, again invokes the intervention of psychical factors which have no definite physiological basis, that is, he regards them as mere illusions or errors of judgment. We must be content to regard the explanation of binocular contrast as doubtful, like that of the so-called "theory of cerebral visual images" (p. 371).

VII. Corporeal or spatial vision—that is, perception of the three dimensions of external objects—is possible with using only one eye. But the solidity of uniocular visual images is not so much an immediate, simple sensation as a true perception or visual judgment, based on light and shade, and on movements of the fixation-point or the head, with corresponding changes in the projection and perspective of the images. When light and dark shading, and the changes in perspective due to

movements of the head or fixation-point are absent, we are incapable of tri-dimensional vision. On looking, for instance, at the drawing of a truncated four-sided pyramid (Fig. 194) the immediate sensation is of a flat geometrical figure in two dimensions. It requires a psychical act to recognise it as the drawing of a body with three dimensions, when, that is to say, we imagine that the small square which represents the truncated apex is nearer the eye than the large square which represents the base of the pyramid. This judgment is arbitrary, because it is founded on no objective character in the drawing. To so great an extent is this true that we can with equal facility regard the same figure as a hollow body in pyramidal form, by imagining that the large square is closer to our eye than the small square. In the same way the diagram of Fig. 195 can be interpreted either as a ladder placed against a wall, or as the under surface of a staircase built on to a wall. In the first case we imagine the right angle *a* to be nearer our eye than the angle *b*; and *vice versa* in the second case. Both judgments are arbitrary, because in such a figure there are none of the accidental features of light and shade by which, on looking at a drawing, painting, or photograph, we obtain the idea of relief, or three-dimensional form. On looking, *e.g.*, at Fig. 196 no one would hesitate in deciding that it was a pyramid with a hexagonal base, as the spire on a church tower; but we are unable to say from objective data whether the flag on the summit of the pyramid is turned towards or away from us, because there is no physiological basis for either judgment.

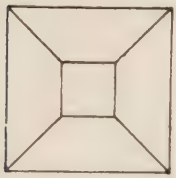


FIG. 194. — Diagram of truncated pyramid with quadrangular base.

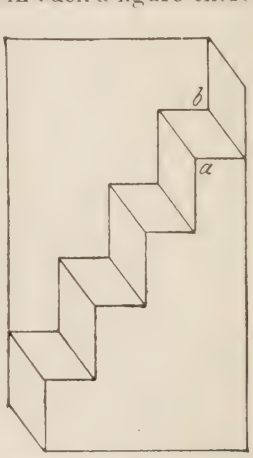


FIG. 195.—Schroder's staircase.

Uniocular people, who are forced always to use one eye, develop the faculty of uniocular tri-dimensional vision of external objects to a remarkable extent, as the blind do the spatial tactile perceptions. In fact, when they learn to draw and paint they are well able to reproduce the physical appearance of objects. Guercino's pictures are remarkable for the relief in which the figures stand out from the background; yet they were executed by the famous painter with only one eye.

None the less it is certain that the perception of the three dimensions is normally much more certain, complete, and direct with binocular vision. Of this we have a simple and very convincing proof in the fact that many people cannot thread a

needle with one eye, even when any ametropia is corrected, though they can do it easily with both eyes.

The fundamental condition of tri-dimensional vision with both eyes consists in the fact that we look at things from two different points of view, so that different perspective images are formed on the two retinae.

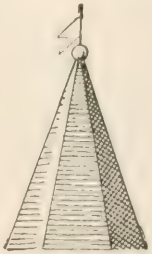


Fig. 196.—Diagram of pyramid with flag. (Bernstein.)

When the images on the two retinae correspond, and the single points of the object fall on identical points, we have no tri-dimensional vision of it. This happens, for instance, on looking at the starry sky, or at any distant object by daylight. When, on the contrary, we focus an object a short distance off, with both eyes, the two retinal images differ the more in proportion as the object is closer to the eyes. For instance, the truncated pyramid shown in Fig. 194 projects very different perspective images on the two retinae from a short distance, as image *R* upon the retina of the right eye, image *L* upon that of the left; in the first the truncated top of the pyramid is deflected to the left, in the second to the right, as in Fig. 197. These two images are incongruous and not com-

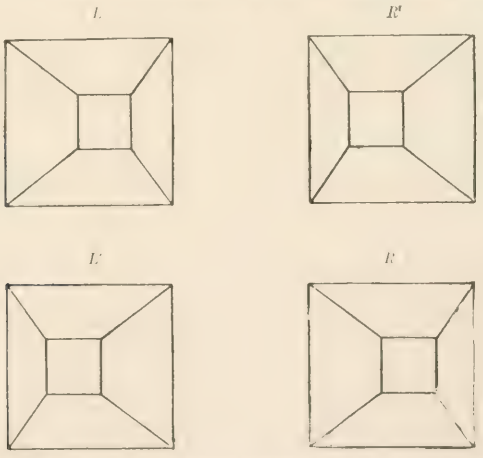


Fig. 197.—Above: right and left perspective images *R L* of a truncated pyramid in relief. Below; perspective images of a hollow pyramid *R' L'*.

pletely superposed; if the big squares of the bases are superposed, the small squares of the apex will be only partially superposed, and *vice versa*. So that if we accommodate our eyes to distinct vision of the base, we shall see the small square of the apex double; if we accommodate for distinct vision of the apex, the large square of the base appears double, since only identical images which fall upon corresponding points can produce binocular single

vision (as above). Experience, moreover, shows that the two images *L* and *R* of the pyramid fuse into the single image of a body in three dimensions. This happens when the two diagrams are examined through the stereoscope.

The physiological explanation of this phenomenon given by Brücke (1841), Prévost (1843), and Brewster (1857) is as follows. In binocular vision the accommodation system of both eyes is constantly altering; convergence and accommodation vary incessantly, so that the images of the several sections of the pyramid fall on identical points of both retinae in quick succession. This constant variation must be regarded as the fundamental condition of binocular tri-dimensional vision. It is as if the eyes explored the different points of the objects more or less distant from us, as by touch we explore the objects around us.

This ingenious interpretation is, however, contradicted by a series of experiments made by Dove (1853), Aubert (1864), Donders (1867), and Bourdon (1902). To obtain a single, solid, stereoscopic image of the two perspective figures *L* and *R* of the pyramid, only the shortest possible illumination, as an electric spark, is required. It is impossible to assume that during such instantaneous illumination there can be any movement of accommodation, or exploring with the eyes (visual touch).

This experiment leads us to ascribe less significance to the absolute correspondence of the retinal points, and to conclude that points in the two retinae which correspond *approximately* may function together. It further leads us to conclude that the correspondence of points is an acquired property, that is, determined by habit. This view is confirmed by the fact that diplopia does not occur in many cases of strabismus because a new set of corresponding points are formed in the retina of the squinting eye. After tenotomy the patients are often disturbed by the appearance of double images for a few days immediately after the operation. It is only the relative and acquired character of the corresponding points that enables us to give any physiological explanation of the stereoscopic fusion of two different perspective images that cannot be superposed, even if we do not entirely exclude Brücke's hypothesis of "visual touch" or the intervention of psychical acts of perception and representation.

Brücke himself fell back later on a psychological explanation (necessarily vague and ill-defined) in which he assumed that it is the task of the brain—as organ of the mind—to complete and perfect the defects of direct visual sensations and endow them with spatial representation.

VIII. The most conclusive proof that binocular tri-dimensional vision depends on the perspective differences between the two uniocular images was given by Wheatstone in 1830 through the discovery of the stereoscope. As shown in the diagram (Fig. 198)

it consists of two mirrors, M, M, arranged at an angle directed towards the median plane of the observer. The two perspective drawings—for instance, that of the truncated pyramid as above—

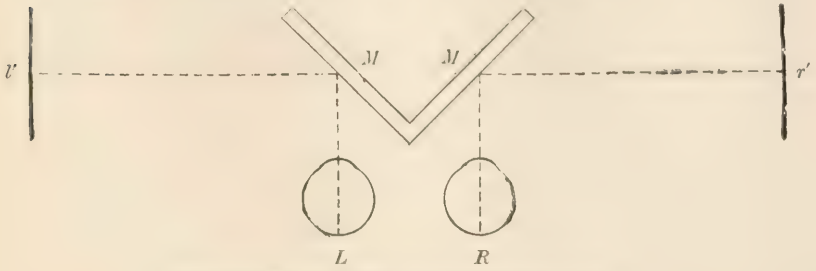


FIG. 198.—Diagram of Wheatstone's mirror stereoscope.

are arranged so that the image R' is reflected into the right eye R, the image L' into the left eye. In consciousness the different points of the two images fuse, although they fall to a great extent on non-corresponding points of the retinae by being successively or simultaneously superposed, and thus the truncated pyramid is seen in perfect relief.

Brewster's stereoscope (1849) is more generally used. It consists of two biconvex prisms PP (Fig. 199), separated by a vertical plane (pp'). Owing to refraction by the two prisms the two images $l'r'$ are superposed into a single complete image (CC') in the plane on which the two visual axes converge.

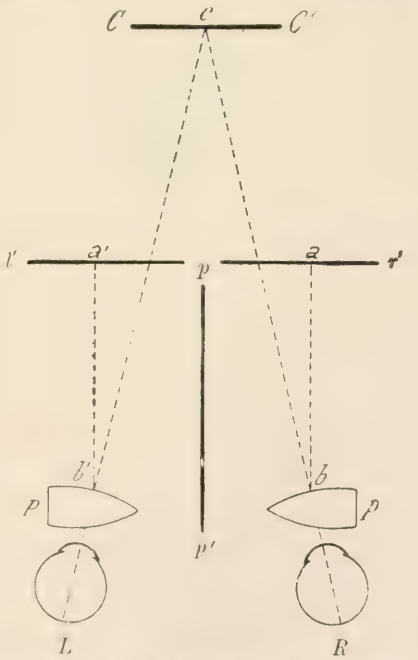


FIG. 199. Diagram of Brewster's prism stereoscope.

It is also possible, without employing any instrument, to fuse two suitable images into one. It is only necessary to keep the two visual axes parallel, that is, to fixate point a with the right eye, point a' with the left; three images will then be seen, each of the lateral with the eye of the corresponding side, while the middle image is seen with both eyes. The two lateral images are flat and two-dimensional, while the third is in relief and three-dimensional.

To facilitate vision in relief without a stereoscope it is as well to interpose a septum between the two drawings (like *tt'* in Brewster's stereoscope) by which the lateral images are cut out. The stereoscope is therefore not indispensable, but it brings about the fusion of the two images without any fatigue of accommodation, and with remarkable precision, while the eyes are in the ordinary position.

By means of photography we can prepare two perspective images of any figure, scene, or landscape for stereoscopic vision. The two photographs are taken with twin cameras, the two lenses being fixed at the same distance apart as the two eyes, viz. 60-65 mm. Experience, however, teaches that a better stereoscopic effect is produced by placing the two lenses farther apart (*e.g.* 70-75 mm.) —the background then appears deeper, and figures and objects seem nearer than the distance at which they were photographed.

In addition to the fusion of the two perspective images in the stereoscope, there is very often an effect known as *stereoscopic lustre*, due, as stated above, to the conflict of the two uniocular sensations.

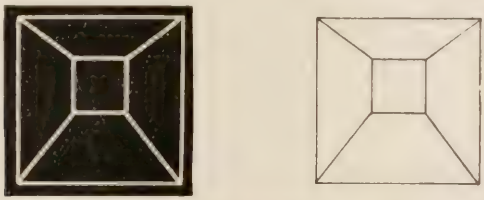


Fig. 200.—Perspective images of two truncated pyramids with quadrangular bases, one white, the other black, which are combined by binocular rivalry into a lustrous stereoscopic image.

If, for instance, we look through the stereoscope at two truncated pyramids (Fig. 200), one white with black outlines, the other black with white outlines, they fuse into a pyramid in high relief of lustrous grey, as though cut out of graphite, with illuminated sides.

If the picture of the left-hand pyramid is placed on the right side, and that of the right-hand pyramid on the left, an inverted relief appears, that is the view of a hollow pyramid seen from below. Such images are known as *pseudoscopic*. The same effect is produced by reversing the position of the double photographs taken for the stereoscope. This is easy to explain, since the figures which give the impression of a hollow pyramid only differ from those which appear as a solid pyramid because the right eye is looking at the figure usually seen with the left eye, and *vice versa*.

Symmetrical objects can be seen in inverted relief with Wheatstone's *pseudoscope*, which consists of two right-angled prisms, arranged as in the diagram (Fig. 201). On looking with both eyes at a solid symmetrical body pseudoscopic vision is obtained. Owing to reflection from the surface of the hypothenuse of the

prisms, the rays from a more distant object fall on the temporal half of the retina, and not on the nasal side as they usually do; in other words, the right eye receives the image which would normally fall on the left retina, and *vice versa*. The fusion of these two images results in complete inversion of the relief of the object.

The same effect is obtained with R. Ewald's katoptric pseudoscope, in which the inversion of the rays to the two eyes is

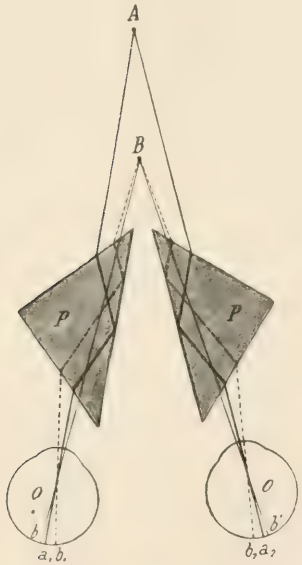


FIG. 201.—Diagram of Wheatstone's pseudoscope.

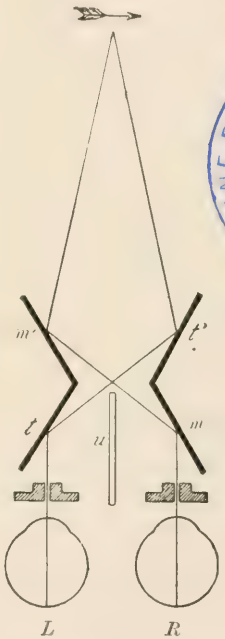


FIG. 202. — Diagram of R. Ewald's katoptric pseudoscope.

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obtained by reflection from two pairs of mirrors, arranged as in Fig. 202.

We do not see far-distant objects stereoscopically, because the difference between the two fixation points is too insignificant to modify the uniocular images perceptibly. Helmholtz succeeded, by means of his telestereoscope, in magnifying the distance between the two eyes artificially, so that he was able to see landscapes on a distant horizon in relief. As shown by Fig. 203 his telestereoscope is only a form of Wheatstone's mirror stereoscope, in which the two drawings are replaced by two mirrors, turned to the horizon, parallel with the internal mirrors. Obviously, under these conditions, distant bodies are seen as if

our eyes were at the distance of the two outer mirrors, and thus a perceptible stereoscopic effect is obtained. In consequence, a landscape viewed with the telestereoscope seems to be nearer than it is in reality, because under ordinary conditions we have an impression of relief in objects only at a comparatively small distance. In this case the relief gives rise to an erroneous judgment of the distance of the objects.

The same principle of the telestereoscope underlies the binocular telescope of Zeiss, in which the mirrors are replaced by prisms; the distance between these is considerably greater

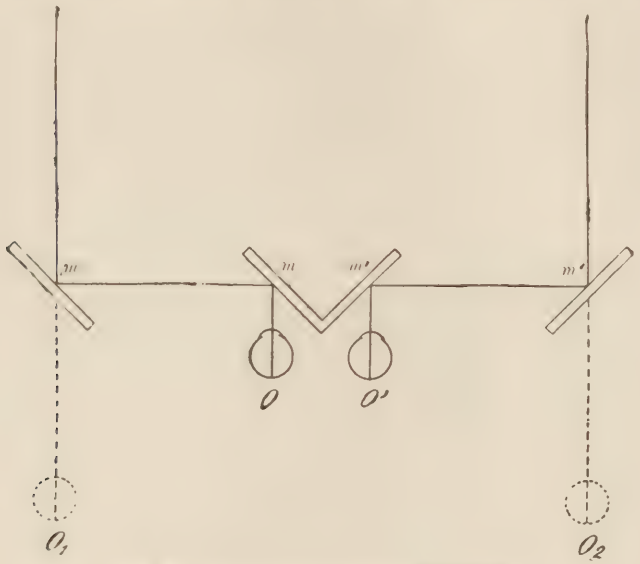


FIG. 203.—Diagram of Helmholtz' telestereoscope.

than that between the two eyes, and the stereoscopic effect is proportionately greater.

To Dove we owe a useful application of the stereoscope for testing the genuineness of bank-notes. We saw that on looking at two identical images in the stereoscope, they fuse into one simple, flat, two-dimensional image. But if they differ in any detail, the observer is at once aware of the smallest discrepancy, either because the two images do not fuse, at the points of incongruence, or because they appear out of the plane, or in front of or behind it.

IX. Visual perceptions and spatial representations of the outer world, *i.e.* the recognition of objects contained in the visual field, and judgment of their size, distance, and characters depend on the sum total of the many and varied visual impressions

produced by stimulation of the individual sensory elements of the retina.

The psychical processes entailed in visual perception of the external world are highly complex, whether they are limited to the identification of objects, or, by a more profound mental elaboration, include judgments as to their characters (size, distance, etc.). This complexity depends on different factors, which are concerned in the transformation of crude sensations into percepts and representations.

(*a*) Visual perception depends not only on elementary sensations, but also on the memory of previous sensations and perceptions: suggestion, recollections, and the association of past with present sensations are weighty factors in the formation of visual percepts and judgments. Every percept, therefore, while it adds something to our experience—that is, to the sum of our memories, is itself in part the result of them. The identification of an object necessarily presupposes exact knowledge of it, but the perception of an unknown thing also connotes the remembering of known objects which it more or less resembles, but from which it differs in some specific character.

(*b*) Visual perception is the result not only of a mental synthesis of the sum total of the countless and manifold elementary sensations excited simultaneously by an object in one or both eyes, but also of those aroused by the rapid alternation and succession of the images due to the movements of the eyes and head, *i.e.* the variety and multiplicity of the sensations aroused by the same object regarded from different points of view.

(*c*) Visual perception is further aided by sensations other than visual, as the muscular sensations, which accompany the movements of convergence, accommodation, and pupillary reactions. The two last come into play in simple uniocular vision, the first only in binocular vision.

The mental synthesis by which the complex simultaneous or successive elementary sensations are transformed into perceptions fails, not infrequently, to correspond with the real objects. The erroneous character of many of our perceptions (distinguished by the name of *optical illusions*) can in a number of cases be readily demonstrated; but they often persist, even when we are convinced of the fallacy. These are interesting, not merely because they are a striking demonstration of the relativity of our visual judgments (and, generally speaking, of the whole of our knowledge acquired through the senses), but also because they enable us to penetrate a little deeper into the analysis of the mental processes which underlie our perceptions.

Most interesting of all is the investigation of our ability, by means of vision, to appreciate the size, distance, and form of the

objects in the visual field. This is known as visual measurement (*Augenmass*).

Judgment of the size of an object is based essentially upon the size of the retinal image. But as objects of very unequal size may produce retinal images of the same size, when they are at such a distance from the eye that they form the same visual angle, it follows that the retinal image can only give us an impression of the *apparent* size of objects, *i.e.* their size in relation to their position. In order to estimate their *real* size, it is necessary to form a judgment of their distance. When the distance at which we regard an object is known by previous experience, we can estimate its real from its apparent size; when, on the other hand, we know the real size of the object, we are able from its apparent size to form a judgment of its distance.

Under ordinary conditions our judgments of the relative size of objects are largely aided by the eye-movements in addition to previous experience, practice, and custom—as we are able by this means to compare the apparent size of the unknown object with that of the known objects near it.

Again, the approximate judgment of the distance of objects is facilitated in uniocular vision by what is known as *aerial perspective*, *i.e.* the degree of precision and clearness of their retinal images and their relative light-intensity, both of which diminish with distance. Binocular vision is further aided by the sensation of effort in accommodation, particularly that due to convergence, which increases with the nearness of the object, and disappears on gazing into the far distance.

Comparison of the two spatial magnitudes is generally made by moving the eyes, so that the images of the two objects fall successively on the same elements of the fovea. In these cases the retina, according to Helmholtz, acts as a measuring calipers, the points of which are successively applied to the ends of different lines. The judgment of their equality or inequality varies with the time that elapses between the two ocular measurements, and with the training of the observer's eye.

When the two spatial objects do not lie parallel—as in the case of two straight lines forming an angle, or two surfaces with different outlines—a successive formation of the corresponding images at the same retinal points is not possible; comparison by the eye becomes difficult, and judgment as to their equality or difference is more uncertain.

Generally speaking, a comparative judgment of vertical distances is far less accurate than that of horizontal differences. Consequently, when we attempt to divide vertical lines exactly, we make greater errors than in dividing horizontal lines. Vertical distances, too, are generally estimated as greater than horizontal distances. To many observers the superior angle of an equilateral

triangle appears greater than the two angles of the base; when we look at a square, the vertical sides seem longer than the horizontal sides. Helmholtz observed that in making a free-hand drawing, by simple measurement with the eye, of a square on a surface perpendicular to the line of sight, it is a common error to draw the vertical lines shorter than the horizontal lines. This error—over-estimation of the vertical sides—varies between $\frac{1}{60}$ and $\frac{1}{30}$ of the total length.

These and other more complicated observations, omitted here for want of space, show (according to Hering) that the power of discriminating size by visual measurement does not depend on the muscular and innervating sensations necessarily associated with the ocular movements, but is essentially dependent on the "local signs" in the retina.

By the *local signs* or *spatial appreciation* of the retina is meant its power of recognising and distinguishing the position of the various points of objects in the visual field. To explain this power we must assume that the excitation of each retinal cone is insulated and conducted separately to the cerebral cortex, and is there separately perceived and differentiated from impulses of the same quality and intensity from other cones. In the same way, we are able to distinguish and recognise the site of contacts in the cutaneous surfaces where tactile sensibility is most delicate. The hypothesis of *local signs* invoked to explain the ability to discriminate between elementary sensations of contact (Chap. I. p. 43), is also applicable to the discrimination of elementary visual sensations produced by identical stimulation of the various elements of the retina, and localised in different parts of the visual field. Just as *local signs* are differently developed in different regions of the skin, so *local retinal signs* are most developed at the fovea—the region of distinct and direct vision—and decline gradually thence towards the ora serrata, where vision is blurred and indirect. Practically, therefore, the development of spatial appreciation in the retina is parallel with visual acuity, since both decline from the centre to the periphery, but theoretically they are quite distinct: spatial appreciation determines localisation, visual acuity, the quality and intensity of visual sensations.

Guillery (1899) attempted to differentiate the *sense of form* from the visual acuity and the spatial appreciation of the retina—the faculty, that is, of recognising and correctly judging the form of objects. This power depends only partially upon the processes by which we estimate size, and is a psychical estimation fundamentally connected with past experience and practice. It follows from Guillery's investigations that the power of recognising more or less simple or complete forms does not depend on their linear extension; in other words, our judgments of the form of

objects do not depend exclusively upon the synthesis of the single, elementary excitations of the retina.

The systematic scientific study of the errors of judgment often made in estimating size by visual measurement has shown that even if the latter is dependent on various anatomical and physiological conditions of the eye it is not due to them alone, but must be based on the psychical process of perception.

Optical illusions, especially of perspective and in estimation of size and distance, have been known since the earliest times. But it was not till the beginning of the last century that they were



FIG. 204.—Optical illusion. (Hering.)

methodically and seriously studied by Oppel, who introduced the term "optico-geometrical illusions." Volkmann, Kundt, and Helmholtz made similar studies; then Zöllner and Poggendorff (1860) drew attention to a new class, that of *illusions of direction*, and Müller-Lyer (1889) to the so-called *optical paradox*. These discoveries and researches were accompanied by speculations as to their cause; various theories were put forward, including that which attributed the cause of the illusions to the eye-movements (Wundt, Delboeuf, Binet), or to irradiation (Einthoven, Lehmann), or to perspective (Tiery, Guye), or to psychological

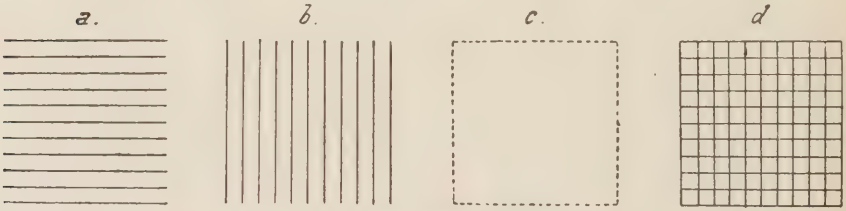


FIG. 205.—Optical illusions. (Hering.)

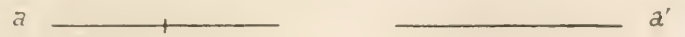
factors (Lipps, Bemessi, Schumann). At the present time optico-geometrical illusions, and the conditions by which they are produced, are an important subject of research in all laboratories of experimental psychology.

We can only cite the most classical examples of these illusions, which have no physiological explanation.

(*a*) Divided distances or spaces constantly appear to us larger than empty spaces (Hering). Many instances of this allusion can be adduced. The space *ab* of Fig. 204 is really equal to the space *bc*, but owing to the dots interposed *bc* appears much larger. The square *a* of Fig. 205, divided by horizontal lines, appears higher than it is wide; square *b*, divided by vertical lines, appears, on the

contrary, wider than it is high. Square *c*, again, like *b* appears higher than its width, but *a* seems higher than *c*; *d*, again, divided by a lattice-work, looks larger than the empty square *c*.

(*b*) The straight line *a*, divided in the middle, is the same length as the straight line *a'*, but appears shorter (Fig. 206). If, however, the mark is moved nearer the end of the line, as in *b*, it gradually begins to look longer than *b'* (Botti). Again, if a dot



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FIG. 206.—Optical illusions. (Botti (*a*, *a'*, *b*, *b'*) and Kiesow (*c*, *c'*).)

is placed at a certain distance above the centre of the straight line, as in *c*, and then moved to the right or left, as in *c'*, the line seems to lengthen gradually (Kiesow).

(*c*) Acute angles are generally judged as greater, obtuse angles as less than they really are (Helmholtz). This error underlies a whole series of optical illusions, the best known of which are illustrated by the diagrams of Hering and Zöllner. In Fig. 207,

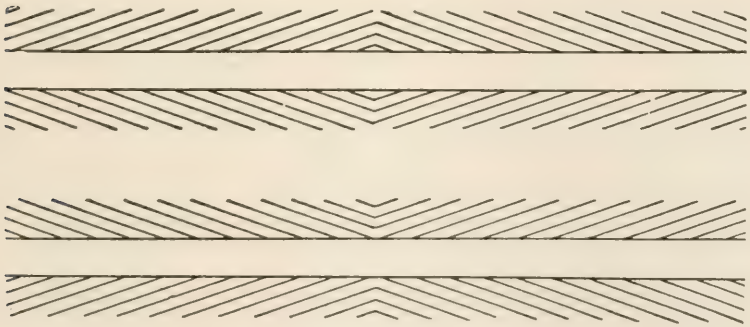


FIG. 207.—Hering's lines: optical illusion.

the four horizontal lines are perfectly straight and parallel, yet the upper pair seem to approximate in the middle and to diverge at their ends, while the lower pair, in which oblique lines are drawn in the opposite directions, appear to diverge at their centres. In Fig. 208, the six black horizontal lines are absolutely parallel to each other, but each pair of lines appears to converge from left to right, owing to the presence of oblique lines which run in the opposite direction. The parallelism of the first and

third lines is obvious, because the oblique lines which cross them lie in the same direction. Interesting variants of this group of illusions were discovered by Préobrajenski. Fig. 209, A, shows a circle in the centre, but it appears to be flattened



FIG. 208.—Zollner's lines: optical illusion.

towards the left, where it is intersected by an acute angle, and more curved towards the right, where it is crossed by lines at an obtuse angle. Fig. 209, B, shows a square with double outlines, but the superior angle on the right appears acute, because it is

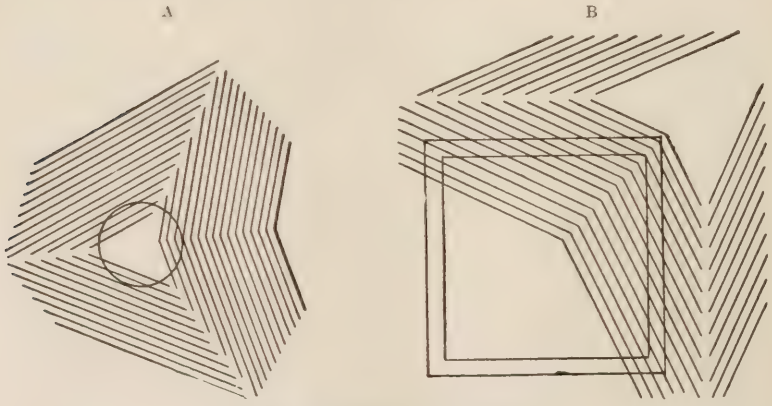


FIG. 209.—Préobrajenski's optical illusion.

intersected obliquely by lines which meet each other at an obtuse angle.

(*d*) Some optical illusions seem due to contrast effects (Müller-Lyer). Two equal lines between two objects of different sizes appear unequal in length. The plainest illustration of this illusion is given by Baldwin (Fig. 210). The dot interposed between

the large and the small black disc is equidistant from each, but it seems closer to the large than to the small disc. Contrast effect also accounts for the fact that the judgment of any direction or dimension is influenced by the vicinity of another different direction or dimension. For example, the upper edge of Fig. 211 is a straight line, but it appears to be bent, owing to the proximity of the lower edge, which is really an obtuse angle (Bourdon).

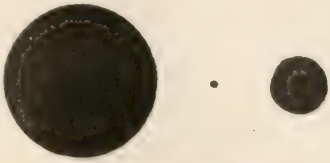


FIG. 210.—Baldwin's optical illusion.

Among the optical illusions of this group, that shown in Fig. 212 (Müller-Lyer) is classical. The two halves of the line



FIG. 211.—Bourdon's optical illusion.

are equal in length, but the oblique lines fall at obtuse angles on the ends of the right half, and at acute angles at the end of the



FIG. 212.—Müller-Lyer's *optical paradox*.

left half; this produces the illusion that the first half is longer than the second half.

(*e*) The illusions recently discovered by Botti in Kiesow's

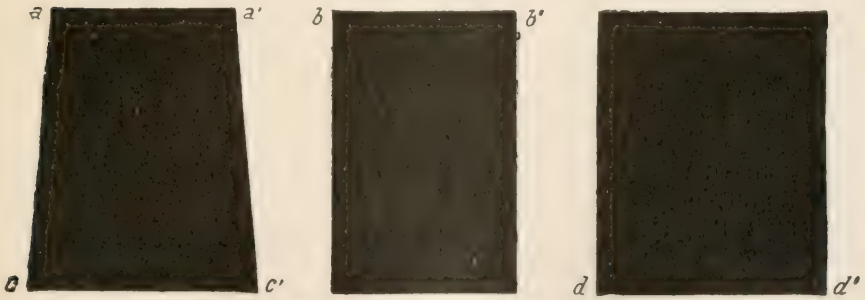


FIG. 213.—Botti's illusions, based on Müller-Lyer's figures.

laboratory are associated with those of Müller-Lyer. Line $a\ a'$ of Fig. 213 is the same length as line $b\ b'$, but appears to be longer. On the other hand, line $c\ c'$ appears less than $d\ d'$, although it is equal to it. In the left-hand figure the upper, horizontal side is

affected by the increasing height of the figure, and seems longer than it is; line $c\ c'$ appears shorter than $d\ d'$, because it is affected by the decreasing width of the figure.

In Fig. 214 the three bands, a, b and c, are really the same height; but b appears higher than the others, and a lower. This is because the parallel oblique lines of b are longer than the vertical lines of a, and as this greater length is taken into account in estimating the height of b, it appears taller. In c this illusion is diminished, because the oblique lines are so close together that they are no longer seen clearly apart, but look like a uniformly

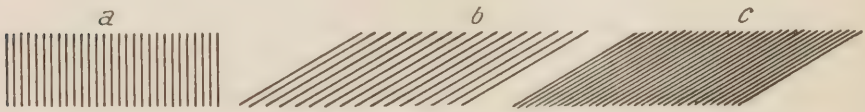


FIG. 214.—Optical illusions. (Botti.)

grey bundle, in which the length of the individual lines is no longer prominent; consequently the influence of irradiation comes in.

In Fig. 215 a number of horizontal lines of equal length are so arranged that they form, as a whole, the shape of a pipe; this produces the illusion that the horizontal lines on the left side become shorter below, and that those on the right are still shorter. This deception arises because the distance between the



FIG. 215.—Modification of optical illusion in last figure. (Botti.)

extreme ends of the pipe makes a greater impression when the figure is taken as a whole than the length of the individual lines.

In Fig. 216 three oblique lines are drawn through a series of equidistant parallel straight lines. They do not, however, appear straight, but seem to be divided into a number of small segments, which lie more or less vertical to the parallel lines, so as to produce a kind of ladder. This illusion is allied to that of Poggendorff, and is due, according to Kiesow, to exaggerated effect of the shortest distance between the horizontal parallels.

The ladder-illusion, reproduced in a of Fig. 217, can be abolished, or much reduced, by introducing hieroglyphs or even dots upon the line that intersects the parallels, as shown in b and c of the figure. In this case, the hieroglyphs or dots attract undue attention to the horizontal line.

These optico-geometrical illusions are closely related to the simpler errors of judgment, known as *irradiation errors*. Even when accommodation of the dioptric system is perfect, it is impossible entirely to avoid vision by diffusion-circles. A luminous point, such as a fixed star, is perceived by us as a small, round, shining surface. Generally speaking, luminous surfaces on a dark background appear larger than they really are, for instance a white square or circle on a black ground seems larger than a black square or circle of the same size on a white ground. The bright edge of a crescent moon seems to form part of a circle of wider radius than its shaded portion. If the lower half of a candle flame is hidden by a sheet of paper, the luminous part seems to spread over its edge, so that the latter appears notched.

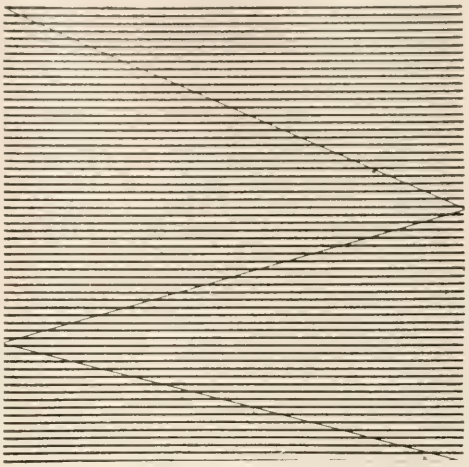


FIG. 216.—Poggendorff-Hering's optical illusion. (Modified by Botti.)

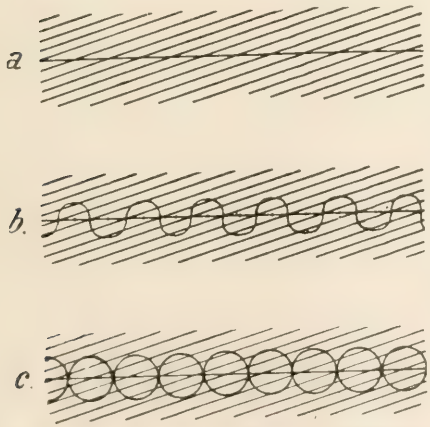


FIG. 217.—Modifications of Poggendorff-Hering's optical illusion. (Botti.)

All these effects, writes Helmholtz, can be referred to the fact that the margins of illuminated surfaces seem to project into the visual field and to invade the adjacent dark surfaces. Obviously, this irradiation, the blurring of contours, and the consequent optical illusions increase with the size of the diffusion-circles which fall on the retina owing to any defect of accommodation. Ovio succeeded in photographing the principal alterations in the images caused by diffusion-circles.

Helmholtz attempted to explain these optico-geometrical illusions partially by irradiation phenomena. Einthoven formulated a theory of the gradual spread of the retinal excitations

from the centre of the fovea outwards, to which he referred certain optical illusions, since a figure cannot be seen simultaneously as a whole without a portion of it falling on a retinal region in which more irradiation occurs. A. Lehmann considered that irradiation is a direct consequence of contrast in brightness, and noted that when this contrast disappears the illusion disappears also. He therefore considers irradiation not only as one cause, but as the sole cause of the illusions. He admits, however, that in illusions of the Müller-Lyer type and others the illusory effect is too great to be attributable entirely to irradiation, and consequently psychological factors cannot be excluded. Botti, too, in a recent memoir, *Optico-geometrical Illusions* (1909)—which summarises the work he carried out under Kiesow's direction—considers irradiation to be one of the factors that comes into play in the genesis of illusions, but does not regard it as the sole determinant. He concludes that illusions are true psychical "facts" of perception. Not only do we localise the illusory phenomenon in the object perceived, but we are further capable of recognising it and comparing it with other previously known objects.

Another phenomenon which in our opinion proves the psychical origin of illusions is the power especially developed in painters of producing a complete and complicated representation of a solid form on paper, with a few rough lines in pencil. This faculty was peculiarly well developed in Leonardo da Vinci, who was able in accidental splotches on the rough wall of a building to see figures of men or animals in different picturesque attitudes according to his fancy.

The transition from these forms of optical illusion, which we may term *constructive*, to true visual hallucinations is easy. "Phantasms or hallucinations are"—in the masterly definition of Joh. Müller—"sensory perceptions that depend on internal causes apart from any external exciting objects."

True visual hallucinations are not those evanescent representations of figures without light or colour which every one can evoke by imagination on closing his eyes; they are actual visions of coloured and luminous images produced by central excitation, and perfectly comparable with the perceptions of real objects present in the visual field which excite the retina.

They are fairly frequent in febrile diseases, in inflammatory states of the brain, in the delirium that accompanies mental diseases, and in certain forms of intoxication. But in conditions of more or less perfect health also they may occur in the half-waking state, in the dreams that accompany sleep, and sometimes even when awake. Blind people too, whose mentality is normal, have been known after extirpation of an eye to suffer from genuine visual hallucinations.

These facts show that the retina is not necessary to the production of the phenomenon we are discussing, and that the central nervous organs alone may be concerned in the genesis of visual phantasms, which are the only cerebral visual images really known to us.

The most interesting and least common visual hallucinations are those of persons, perfectly sound in mind and body, who have the faculty on closing their eyes of seeing visions that are perfectly comparable with the images of real objects. Cardano, Goethe, and Johannes Müller possessed this power.

"In 1828," writes Müller, "I had occasion to discuss with Goethe this subject, which was equally interesting to us both. As he knew that when I lay down quietly with my eyes closed images readily shaped themselves before me though I was not actually asleep, since I was quite able to observe the figures, he was very curious to know how these images were formed in my mind. I told him my will had no influence on the production or on the changes of those figures. . . . Goethe, on the other hand, was able to choose the subject at will, but the changes then developed, apparently involuntarily, but in regular and symmetrical order. Here is the difference in the two natures—the one endowed with a wealth of poetical imagination in the highest degree, the other directed to the investigation of reality and of natural processes."

X. Secure elsewhere within the bony walls of the orbit, the eye is protected in front by the lids, which are able to close rapidly, in order to keep out excess of light, or to lessen the effect of sudden mechanical shocks.

According to Exner the hairs of the eyebrows and eyelashes are the most sensitive organs of the whole body. Their importance in the protection of the eye is therefore obvious; the eyelashes are peculiarly adapted to prevent the penetration of dust particles from the air into the conjunctival sac; the hairs of the eyebrows —apart from their importance in expression—keep the perspiration of the forehead away from the eyes, and moderate the action of the light rays from above. The lashes are continually lubricated by the secretion of the adjacent Meibomian glands which open near their bulbs.

The eyelids close automatically and remain closed during sleep; they also shut reflexly in the waking state to external stimuli. Winking may be caused by stimulation either of the optic or of the trigeminal nerves; the reflex is always bilateral, even when the stimulus acts only on one eye—unilateral winking is normally a purely voluntary action. This is the case not only in men and apes but also in carnivora (dogs, cats); on the other hand, in herbivora (rabbits, guinea-pigs) and in birds and amphibians (frog) reflex winking either by the lids or by the

nictitating membrane takes place only on the stimulated side (Langendorff).

Reflex winking occurs when the optic nerve is stimulated by a sudden illumination or by the rapid approach of some foreign body to the eye: or by mechanical or chemical stimulation of the end of the trigeminal nerve, by contact with the lashes, conjunctiva, or cornea, or by the action of irritating gases on the latter.

The reflex effect increases with the intensity of stimulus. Gentle stimulation produces contraction only of the pars palpebralis of the orbital muscle, which is innervated by the facial nerve; when the stimulation is stronger, other muscles, as the corrugator supraciliaris, are involved.

Apart from accidental stimuli there is a periodic blinking of the lids, which may be frequent when these nerves are irritated by cooling or drying of the corneal and conjunctival surfaces of the eyeball. The closure of the eyes is followed by their rapid opening, effected by the levator palpebrae superior.

Nothing is definitely known of the localisation of the centre of the lid reflex. According to Nickell it lies in the upper part of the medulla oblongata. The cortical centre of the orbicularis probably comes into action during voluntary uni- or bi-lateral closure of the lids; but as a matter of fact the lid reflex is not abolished or affected by its extirpation in the dog (Eckhard).

The action of the striated muscles is reinforced by that of the smooth muscles of the eyelid, described by H. Müller, which are kept in tonic contraction by the influence of the sympathetic. Section of the cervical sympathetic produces narrowing of the palpebral fissure and slight retraction of the eyeball; its electrical excitation produces, besides dilatation of the pupils, widening of the fissure (*lagophthalmus*) and prominence of the eyeball (*exophthalmus*).

In order that the cornea may retain its perfect transparency it is essential that it should be continually irrigated by a thin layer of lachrymal fluid, which keeps it clean and prevents it from drying. Tears are the secretory product of the lachrymal gland, which is an elongated and flattened mass, the size of a small almond, situated in the upper and outer part of the orbit, in contact with the superior and external recti muscles. The anterior and inferior portion of the gland is separated from the rest by an aponeurotic layer, and may be regarded as a gland in itself (glandula lacrimalis inferior). Other smaller glands lie along the conjunctival fornix, 30 to 40 in the upper, 6 to 8 in the lower sac.

The lachrymal are similar to the salivary glands, *i.e.* they are ramified tubular glands. The secreting cells that line the alveoli present during rest and after activity, *e.g.* in crying, suffer changes

similar to those described in speaking of the salivary glands (Vol. II.). The epithelium of the secretory ducts has no rod structures or cilia. The ducts of the two larger glands, 10 to 12 in number, pass obliquely through the mucous membrane and open in the upper and outer part of the conjunctival fornix.

The chemical composition of *tears*, *i.e.* the mixed secretion of the lachrymal glands as a whole, was first analysed by Fourcroy and Vauquelin (1846). It is a very watery fluid, alkaline in reaction, strongly saline in taste; so far as is known, it contains no enzymes, but has a little albumin in solution, with mucus, sodium chloride, and traces of sodium carbonate, alkaline phosphates, and alkaline earthy salts. Under the microscope it is seen to contain epithelial cells thrown off from the lachrymal ducts and the conjunctival surface, and fat droplets secreted by the Meibomian glands. The daily output of secretion is estimated at about 3 grms. for each eye.

The lachrymal secretion is continuous, but increases whenever certain stimuli act reflexly upon the lachrymal glands. The lachrymal fluid spreads from the upper and outer part of the conjunctival sac by capillarity, over the whole of the anterior surface of the eye, between the palpebral and bulbar layers of the conjunctiva, to the inner angle of the eye—the so-called lachrymal lake. During winking the lachrymal fluid on the corneal surface is renewed, and its passage towards the lachrymal lake facilitated; the overflow passes into the so-called lachrymal points and through the ducts into the lachrymal sac, whence it eventually flows into the nasal canal.

When the secretion is not excessive, as it is in crying, the tears do not pass beyond the free margins of the lids, because they are kept back there by the sebaceous secretion of the Meibomian glands. Schirmer (1902) observed on 50 individuals in whom he had excised the lachrymal sac that the tears even then seldom or never overflowed the edge of the lower lid, unless an increase of secretion was produced artificially. It is therefore probable that under normal conditions there is no drainage through the lachrymal canals, evaporation from the free surface of the eye and conjunctival absorption being sufficient to remove the tears. It is only when the flow of tears exceeds the normal that they collect in the lachrymal lake.

Lachrymal secretion, like the movements of the lids, is normally a reflex act produced by peripheral stimuli. These may act on the optic nerve (bright light) or on the trigeminal (drying by evaporation or by currents of air, chemical stimulation by irritating gas, mechanical stimulation by particles of dust or other foreign bodies). Chemical or mechanical irritation of the nasal mucosa also produces a reflex lachrymal secretion. Unilateral stimulation of the optic nerve causes a flow of tears in both eyes,

unilateral stimulation of the trigeminal nerve usually produces a flow of tears only upon the same side (Wilbrand and Sänger).

From the lachrymal secretion reflexly produced by peripheral stimuli we must distinguish that evoked by central impulses, viz. tears in yawning or crying.

The origin of the nerves to the lachrymal glands and the centre of reflex or direct lachrymal secretion is not yet known. According to the investigations of Campos (1877) the ramus lachrimalis of the trigeminal nerve contains secretory fibres that do not come from the facial nerve; but Goldscheider (1895), Uthoff (1886) and others noted that in total paralysis of the facial the flow of tears in weeping is absent on the paralysed side. According to Eckhard (1867) the centre for lachrymal secretion lies in the upper part of the medulla oblongata; according to Seek it is situated between the 6th cervical segment and the lower end of the spinal root of the trigeminus; according to Bechterew and Mislawsky in the corpora quadrigemina.

How tears flow through the lachrymal passages is not yet settled. Haller first stated that the tear-points took up the tear by capillary attraction and conducted them to the lachrymal sac, thus contradicting the hypothesis of Petit, that the lachrymal apparatus acts as a siphon. Hounault, E. H. Weber, and v. Hasner held that the inspiratory current of air causes suction of the tears collected in the lachrymal lake. Against this hypothesis we have the fact demonstrated by E. H. Weber that on introducing a small manometer into one of the tear-ducts no fall in the level of the fluid can be observed during inspiration. It is certain that winking accelerates the flow of tears into the lachrymal passages. If a fluid covered with aniline be introduced into the lachrymal lake, it is rapidly absorbed if the eyes are closed repeatedly, but very slowly if the lids are kept open. It is therefore obvious that the orbicularis muscle and Horner's muscle exert some action on the penetration of tears into the lachrymal passages. But how do they do so? According to Richter and Schmidt, closing the eyes dilates the lachrymal sac and allows it to fill; Arlt and Moll, on the contrary, hold that this compresses, and thus helps to empty it. Henke admitted both these interpretations, and assumed that during the closure of the lid the lachrymal sac is dilated by contraction of the palpebral portion of the orbicularis, so that the tears are aspirated, and during opening of the lid the lachrymal or Horner's part of this muscle contracts, and the tear-sac is compressed. Gad contradicted this last statement of Henke, and assumed that contraction of the sac is due to its elasticity.

Scimeni, on introducing a small tube of fluid through a fistula in the lachrymal sac, found that the fluid was rapidly aspirated into the sac on closing the eyelids, and slowly returned to the tube

on opening them. It is not apparent why, under normal conditions during the dilatation of the sac produced by the contraction of the orbicularis, the tears should be absorbed by the narrow tear-points rather than sucked into the sac from the nasal passage, and why during its contraction they should not again flow back through the tear-points. In partial explanation of this fact, it is well to remember that the nasal extremity of the lachrymal canal is closed by a valve described by Hasner, which prevents a back-flow of tears, but permits them to pass into the nasal cavity.

XI. In conclusion we must glance at the properties and origin of the *humours of the eye*, as well as the *intraocular pressure* to which they give rise.

The aqueous humour is a clear, colourless fluid, alkaline in reaction, of a specific gravity that varies between 1·0034 and 1·0060, and contains about 0·86 per cent solids, 0·045 per cent of which consist of protein—albumin and globulin. The normal fluid of the eye contains no fibrinogen, but sugar up to 0·03-0·05 per cent. Its osmotic pressure, according to the researches of several recent workers, is higher than that of blood. If the anterior chamber of the eye is artificially emptied, it fills again rapidly with fresh fluid, which is not, however, exactly the same as the normal, because it contains more protein and also fibrinogen, so that it may coagulate spontaneously. But six hours after evacuation it again has all the properties of normal aqueous humour. If, after the puncture, the sympathetic be stimulated, or a solution of suprarenal extract introduced into the conjunctival sac—both of which produce vascular constriction—these changes in the property of the newly-formed aqueous humour do not occur.

The origin of the aqueous humour has been and still is much discussed. According to Leber and many others, the ciliary processes are the anatomical structures that produce it. The arguments in favour of this theory are as follows:

(*a*) Extirpation of the ciliary body along with the iris causes total disappearance of the intraocular eye-fluids (Leber, Deutschmann); on the other hand, congenital absence or complete removal of the iris does not hinder the formation of this fluid.

(*b*) If, after connecting the posterior chamber of the eye through the pupil with a manometer, the pressure of the latter is made equal to that inside the eye, it is found that pressure rises. If the aqueous humour is allowed to escape, by perforation of the cornea, so that the iris is pushed forward against the posterior corneal surface, it will be seen that this condition remains permanent; so too, in cases in which the pupil is adherent to the lens capsule, the iris is pushed forward. These facts are easily explained on the assumption that the aqueous humour comes from the posterior chamber of the eye, *i.e.* is produced by the ciliary processes.

Ehrlich disputes this theory. In 1882, he observed in the rabbit that after injection of fluorescin a greenish, fluorescent line appeared at the margin of the iris and spread towards its base. No flow of fluorescin from the pupil can be seen previous to the appearance of this line. From this Ehrlich concluded that the aqueous humour is produced, not from the ciliary bodies, but from the anterior surface of the iris. On the other hand, this is also observed on dead animals, when fluorescin is injected into the veins (Ehrenthal), and sometimes, when the ciliary bodies are hyperaemic, fluorescin flows from the pupil before Ehrlich's line appears (Nicati).

Another theory put forward by Hamburger (1899) assumes that the aqueous humour under normal conditions is produced by the anterior surface of the iris, but that when the flow is exaggerated the ciliary processes also share in its formation. He adduces in support of his theory the observation that aqueous humour is already present in the foetal eye, even when the membrane that occludes the aperture of the pupil is still present.

The various authors again disagree as to the *nature* of the physiological process that gives rise to the formation of the aqueous humour. According to Leber it is due to filtration from the blood-vessels. Against this view, however, Hamburger and Bottazzi point out correctly that there are marked differences between the physical and chemical properties of the aqueous humour and of blood plasma, which are inexplicable if we assume it to be formed by a simple process of filtration. It has, in fact, a higher osmotic pressure and electrical conductivity than serum, besides considerable differences in its chemical constitution as compared with serum. Accordingly, we must assume that the fluid of the eye is formed by a process analogous to *secretion*. In support of this theory is the fact repeatedly observed by many authors that lesions of the ocular nerves (sympathetic and trigeminal) produce changes in the constitution of the aqueous humour. The question next arises whether we are to assume that there is a genuine secretory process effected by a differentiated glandular epithelium, or by a process similar to that concerned in the formation of lymph (*supra*, Vol. I.), that is, by the activity of the endothelial elements of the walls of the blood capillaries, as suggested by Angelucci (1902).

Once formed, the aqueous humour does not remain stationary inside the chambers of the eye, but as it is formed a portion of it is reabsorbed by other parts of the eye, and returned to the lymph spaces. This hypothesis is based mainly upon the observation that the renewal of the humour takes place a comparatively short time after it is evacuated. Obviously, however, no logical conclusions can be deduced from this in regard to the normal circulation of the fluid. The most important objection

to it is evidently the fact that after puncture of the cornea there is no longer any pressure in the anterior chamber, so that the rapid production of the fluid may be interpreted as the effect of the disappearance of pressure.

Leplat attempted to settle the question by experiment; he injected liquid paraffin into the anterior chamber of the eye in rabbit, in order to hinder the outflow of aqueous humour, and then connected the vitreous body with a manometer. He found that immediately after injecting paraffin the manometer showed a normal, intraocular pressure, but then rose suddenly; in one minute some 4 cmm. of fluid passed into the manometer. From this it may be concluded that the content of the anterior chamber of the eye is renewed in about 75 minutes in the rabbit, and in about 50 minutes in man.

The same questions arise in regard to the *absorption* of the aqueous humour; in the first place by which structure is it absorbed, and in the second how does absorption take place? Without entering on the details, it may be stated that it is now generally held that absorption takes place in the angle formed by the iris and the cornea, through the trabeculum of the so-called ligamentum pectinatum iridis. This conclusion was arrived at by injecting different fluids into the anterior chamber. It was also found that the rate at which absorption of the injected fluids takes place under these conditions is proportional to the pressure at which the injection is carried out (Hering, Leber, Adamük, and Jessner), whence it has been concluded that the normal process by which absorption of the aqueous humour takes place is not secretion, but filtration, due to excess of intraocular pressure over that in the periocular lymph spaces.

A similar conclusion has been arrived at by injecting coloured fluids or suspensions of very fine powders into the anterior chamber. It is, however, found that in addition to the angle of the iris its anterior surface is also infiltrated with the injected granules, and from this it is assumed that the iris also takes part in the absorption of the aqueous humour.

Certain experiments of Grandis and Moret (1901) on the rabbit's eye, however, tend to show that the absorption of the aqueous humour is not due to filtration. They connected the anterior chamber with a manometer, and then observed the variations of pressure for a considerable time, and found that it first increased rapidly, and then more slowly, till after about half an hour it became stationary, which—according to these authors—cannot be accounted for on the view that the formation of aqueous humour is an effect of simple filtration. In a further series of experiments they found that if the pressure is artificially raised after it has become constant, a larger amount of fluid is absorbed than has been added, so that after a certain time the

intraocular pressure becomes less than it was at the outset of the experiment. This tends to show that the absorption of the humour is not due to simple filtration.

The *vitreous body* consists of a trabecular skeleton of collagenous substance, the meshes of which contain a fluid of approximately the same physical and chemical properties as the aqueous humour; it also contains a mucoid.

It is generally held that the vitreous humour is also a secretion from the ciliary processes. Nothing definite is known as to the circulation and absorption of this fluid; but it is generally assumed that it circulates and is renewed exceedingly slowly. Schwalbe demonstrated that the perivascular lymph spaces of the branches of the arteria centralis retinae communicate directly with the hyaloid canal. After injecting coloured substances into this canal they reappear in a short time in these lymph spaces (Leber).

The pressure in the eyeball is, as will readily be understood, one of the most important factors in the correct function of the dioptric systems of the eye. This pressure depends (*a*) on the tension of the intraocular contents; (*b*) on the resistance opposed by the elastic walls of the eyeball. As the latter is constant, or probably varies but little within physiological limits, we must—to understand the oscillations of intraocular pressure—consider the factors which determine the amount of fluid contained in the eye, and the pressure that prevails in the intraocular blood-vessels.

The height of intraocular pressure varies under normal conditions in man and animals between 20 and 30 mm. Hg.

The methods employed in measuring intraocular pressure are of two kinds: manometers (in animals) and tonometers. The former, by means of special cannulae, are brought into direct connection with the interior of the eye. The latter exert pressure on the outer wall of the eyeball by a small plate, so as to flatten it (A. Fick). By measuring the force necessary to obtain a certain degree of flattening, it is easy to calculate the pressure within the eye.

According to Bottazzi and Sturchio (1906) the fluids of the eye contribute effectively to the maintenance of the normal intraocular pressure, owing to the fact that their molecular concentration is higher than that of the blood. On analogy with the phenomena of turgor in plant cells (Pfeffer) these fluids continuously attract water from the outside, that is through the coats of the eye—which must accordingly be semipermeable—and thus increase in volume.

As we stated above, the intraocular pressure is also in relation with the pressure in the blood-vessels. In fact, oscillations of intraocular pressure which correspond exactly to those of the blood-pressure have been described. These pulsations are

particularly prominent when the intraocular pressure is very high.

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CHAPTER IX

PSYCHO-PHYSICAL PHENOMENA OF CONSCIOUSNESS AND SLEEP

CONTENTS.—1. The range of mental life includes unconscious as well as conscious processes. 2. States of complete and incomplete consciousness. 3. Subconscious activity; its great importance in relation to conduct and genius. 4. Development and integration of the mind a function of the subconscious, based on psycho-physical processes as distinct from conscious processes. 5. Disintegrations of personality (double consciousness, secondary personality, alternating personality). 6. Physiology of sleep. 7. Theories of sleep. 8. Psychology of sleep. 9. Dreams. 10. Telepathic phenomena. Vitalism and materialism. Bibliography.

IN analysing movements and sensations we have investigated the two extreme phases, terminal and initial, of the processes of animal life. We must now examine the intermediate phases of these processes, which take place in the nervous system, and which include the whole of the complex phenomena that occur as we pass from the Unconscious to the Conscious, in which *objective* or purely physiological factors assume a *subjective* or psychological character.

We know that the nervous system is the substrate of the functions of animal life, and that it brings about the physiological unity and reciprocal interdependence of the organs, on which the psychological unity, expressed in the phenomena of the *Ego*, or Consciousness, depends.

Owing to its pragmatical rather than to its intrinsic philosophical value, the hypothesis of "psycho-physical parallelism" enables us still to deal with positive phenomena and controllable laws, without crossing the threshold of metaphysics (Chap. I. 2-3). By it we may conclude that each psychical phenomenon or state of consciousness has a somatic basis, a concomitant neural process; and we may leave to metaphysicians the attempt to solve the problem of how and why, during life, the "soul"—whether considered as an entity or as a complex of psychical phenomena—must remain intimately connected with the body, and act with or parallel to it.

Generally speaking, we class as *psycho-physical phenomena* all those which we know both subjectively and objectively, which,

according as they are examined by internal or external observation, are presented to us with totally different characteristics, but which are reciprocally, in Fechner's words, interdependent like the two surfaces, the concave and the convex, of a sphere; which consist in material changes and correlated psychical alterations, corresponding to the objective and subjective sides of "a unity with two faces" (Bain); which appear introspectively as *states of consciousness*, extrospectively as *excitations* or *states of nervous activity*.

In the preceding chapters we have especially considered the objective side—that is, the physiology of neural activity—and were we now to attempt any adequate analytical examination of the subjective side, that is of mental activity, we should trespass on psychology and be compelled to renounce the experimental method and to adopt that of introspection, by which alone it is possible to analyse the highest and most complex mental processes. But intermediate between physiology and classical psychology there has recently been developed a new branch of science, the so-called *psycho-physical* or *physiological psychology*, which has abandoned metaphysical speculations about mind, the nature of the soul, and the higher mental operations, and is occupied with the study of elementary psychical phenomena, though it does not confine itself to the consideration of these, but endeavours to evoke them under special pre-determined conditions. The experimental method as applied to the study of mental facts permits us to analyse their constituent elements more readily and to determine their causations and variations under different conditions. We have already applied this purely physiological method in the study of the nervous system and special senses, to bring out the connection between mental phenomena and their somatic basis, to analyse the varied modality and quality of sensations in temporal sequence and spatial coincidence, to measure the duration of elementary psychical processes, and so on. But to a certain extent this involves the analytical study of other more obscure and complex phenomena, associated with different degrees or forms of consciousness, with the processes of attention and memory, and with the reciprocal action of sensations, *i.e.* the manner in which the simplest mental states influence each other, and are reciprocally evoked, associated, and inhibited.

In order not to invade the field of pure psychology, we must confine ourselves to the most accessible functions of mental activity in so far as they are connected with neural activity, keeping always to positive knowledge, without attempting any solution of the higher and more abstract metaphysical problems.

I. Any one who undertakes the study of *psycho-physical phenomena* observes as one of the cardinal facts that not all stimuli, or states of neural activity, cross the threshold of

consciousness—in other words, acquire a subjective aspect and present themselves to introspection. The greater part of the elementary nervous activities, which consist in simple responsive or reflex acts, fulfil their protective or regulatory functions in the body within the region of the *unconscious*. This can be observed not only in all the nervous actions destined to influence and control the functions of the visceral organs, but also in a great number of the excitations that affect the organs of animal life. During the activity of the senses, again, the psycho-physical phenomena, the physiological processes that reach consciousness, include only a small part of those in which the sensory system is concerned, those, namely, which are the object of attention. So that in our nervous system the unconscious and the conscious are very unequally divided; the neural excitations presented to introspection as part of the *ego* are few in number, and do not permanently occupy the same position, but are constantly displaced according to the direction of attention and the current of thought. Whatever remains outside the focus of attention is not clearly apperceived, and may be provisorily regarded as unconscious. So that if the mind consisted exclusively of the sum of the phenomena of which we are fully conscious, the province and scope of our mental life would be poor and narrow indeed.

But when we come to examine the nervous processes that do not reach consciousness, it is evident that they depend in many cases on the same complex mechanisms as those that become conscious, and have the same specific characters. When, for instance, we walk along a road, completely absorbed in what we are going to say to the person we are about to visit, the locomotor mechanism carries out its functions perfectly without assistance from our will or consciousness. But our movements, guided more especially by sight, are not entirely comparable to a regular series of simple reflex actions, because they are continually altered and modified in order to avoid obstacles, such as vehicles and people on the road; in a word, we adapt our muscular acts, according to circumstances, to the end we have in view. The same applies to an expert violinist who is executing a piece of music. While his attention is wholly absorbed in the current of multiple auditory sensations combined in successive order, his eyes glance rapidly down the page, without waiting to perceive the individual notes, and his hands automatically and unconsciously perform a long series of varied movements, of a complicated and difficult kind, co-ordinated to produce an artistic effect with the minutest gradations of tone, intensity, and musical expression.

Now the only possible scientific criterion by which we are able objectively to distinguish psychical manifestations from purely mechanical phenomena is their perseverance in an aim, their

adaptation to circumstances, their choice of the means best suited to an end. The physiologist makes constant use of this test when he compares the degree of intelligence in different animals in the zoological scale, and attempts to define the psychical or the purely mechanical character of the functions of the various nerve-centres. In this connection we may refer again to the movements of which the spinal frog (Vol. III. pp. 335-341) and the bulbo-spinal animal (pp. 351-5) are capable, which led us to conclude that consciousness is not localised exclusively in the brain, but is diffused throughout the cerebro-spinal axis; and that an animal in which the brain-centres are mutilated is not deprived of sensibility and of the power of carrying out many reflex acts which present a teleological character—that is, are adapted to circumstances and vary with variation of environment, as in removing injurious stimuli.

Strictly speaking, these acts cannot be called *conscious*, because the brainless animal has no perceptions, representations, or volitions—which are the condition of *states of consciousness*. Still—granting the teleological responsive and adaptive character of its actions—it must be vaguely aware of elementary cutaneous and muscular sensations, which suffice to make up a lower form of consciousness (Pflüger's so-called *spinal animal*), consisting in a synthesis of sensations which are able, however indefinite and rudimentary, to initiate co-ordinated responsive acts, adapted to a purpose, and therefore of the same type as conscious and voluntary acts.

In the ordinary language of physiology the expressions "unconscious sensations," "unconscious feelings," frequently recur and seem to be nonsense and a contradiction in terms, seeing that sensations and feelings are fundamental elements in consciousness; but they become intelligible and practically justifiable in so far as they signify that there are different forms and degrees in consciousness. We can readily distinguish the states of consciousness that form the content of the *ego*, on which we direct our attention by taking these states as the objects of our thought, from the active states of sensibility which operate outside the range of attention. These last may justly be termed in a broad sense *unconscious sensations and feelings* because they lie at the threshold of consciousness, *i.e.* of the sensorial ego.

These nervous processes, accordingly, have the same specific characters, produce the same results, and fulfil the same functions as conscious sensory processes; it follows that they come into the range of mental life, and even constitute by far the largest part of the integral content of the mind.

In support of this theory it is easy to show that conscious and unconscious states can be reciprocally transformed into each other, and that there is a constant exchange between them.

We have seen that walking consists in a series of complex movements which can be carried out automatically with ease and precision even when we do not attend to them; but these movements are the final result of a long and tedious series of voluntary efforts which the child carries out in learning to stand on its feet and to move by alternate steps so as not to fall, until it is able to walk safely without the guidance of attention. To this it may be objected that the new-born infant is incapable of walking because its complex nervous mechanisms are not yet fully developed. The chick, in fact, can hop and peck at its food without preliminary attempts, because the systems subserving these functions are already well developed when it cracks the egg-shell. But turn to the violin-player, in whom an hereditary transmission of the artistic capacity is at most virtual, and not actual. Long and arduous voluntary efforts, fatiguing attempts and graduated exercises, must be faced by the would-be violinist before he acquires the full mastery of the complicated neuro-muscular mechanism necessary to the perfection of his art—which is attained only when he can find, without the slightest voluntary effort, the multiple centrifugal paths for the impulses required in the execution of the several musical sounds from which harmonic combinations and melodic sequences result.

This is a classical example of the gradual transformation of conscious and voluntary into unconscious and mechanical acts by practice and habit. We do not know what the organic and functional changes due to habit—that is, the frequent repetition of the same act until we have acquired the faculty of executing it perfectly—consist in. To account for them in any way, we must suppose that as the result of repeated exercise certain definite neural paths are rendered more pervious, and conduction through them is facilitated, while the spread of excitation to other collateral paths is rendered more difficult. This hypothesis explains why the habit that results from practice makes our movements easier and simpler, less fatiguing and more perfect; why a less amount of attention is needed for their performance; why, finally, the acts that were originally conscious and voluntary gradually become unconscious and mechanical.

"In action grown habitual," says William James, "what instigates each new muscular contraction to take place in its appointed order is not a thought or a perception, but the *sensation occasioned by the muscular contraction just finished.* A strictly voluntary act has to be guided by idea, perception, and volition throughout the whole course. In an habitual action, mere sensation is a sufficient guide, and the upper regions of brain and mind are set sufficiently free."[1]

It is just this *simple sensation*, capable of promoting complex

[1] *Principles of Psychology*, William James, 1890, i. p. 115.

effects of a teleological character, without active intervention of the higher cerebral centres—*i.e.* without transformation into perception, representation, and volition—that we term *unconscious* in the widest and most general sense of the word.

As conscious psychical processes may become unconscious by exercise and habit, so, evidently, many unconscious psychical processes may become conscious when we direct our attention to them. It is more remarkable that, independently of the attention, an unconscious operation may unexpectedly lead to a conscious intellectual result.

It is sometimes impossible to recall the name of a person, however strenuously we flog our memory; but if we cease to think about it, and turn to other things, the name sought in vain may presently be remembered. Again, the utmost effort of intelligence may fail to reveal to us the relation and interdependence of certain observed phenomena or the solution of a long-considered scientific problem: after giving up the attempt and turning our thoughts to another subject, it sometimes happens that the solution vainly sought presents itself clearly and convincingly on the mental horizon, without conscious effort.

The history of science is full of such examples: the discovery of the principle of the rotating magnetic field by Galileo Ferraris is a striking proof of this. "One evening in August 1885" (writes his biographer, R. Arnò) "he went as usual for a walk, wandering alone in the neighbourhood of the Cernaja barracks in Turin. He was musing as he went, in a brown study. And giving rein to the natural sequence of his thoughts he began to reflect on the analogy of optical and electro-magnetic phenomena, and on the origin of light electrically and circularly polarised, which depends on the combination of two simple oscillatory movements of the ether. A flash of genius arrested him; and he asked himself whether a similar effect could not be brought about by substituting the variations of two superposed magnetic fields for the two component oscillations."

These are typical examples of a direct transformation of conscious into unconscious neural processes, and then of the latter into the former without the intervention of attention. "Unconscious activity," as Höffding justly remarks, "has effected that which direct and assiduous mental labour could never have accomplished." In these cases, conscious initial work is the first condition of the effect; the subsequent unconscious work is the means that consummates the action, by which the final result desired is attained in a well-defined and clearly conscious form.

Accordingly, it cannot be denied that unconscious neural processes have the same character as conscious processes, and that the range of psychical life is not confined to the latter, which form the content of the empirical or sensorial self, but

also includes the former, which do not pass the threshold of consciousness, either because they are incapable of crossing it, or because they are carried on beyond the range of attention.

II. The fundamental importance of the distinction between *conscious* and *unconscious* makes it advisable to inquire more minutely into these concepts, and to subject them to a strict analysis.

The word "conscious" expresses a positive idea of which practically every one grasps the significance, but it is by no means easy to give an adequate definition of it. It is not enough to say with Wundt and Höffding that a conscious phenomenon consists in the association or synthesis of a multiplicity of sensations or elementary psychical processes; it is necessary to add that this synthesis must constitute an internal experience, which leads us to become aware of an object, or to feel something. The really conscious phenomenon is always a phenomenon of perception, with the inherent attribute of definiteness or lucidity, so that the object of experience is recognised as something distinct from the *ego* that perceives it.

From the subjective or psychological point of view, it is therefore impossible to speak of a state of consciousness, or of conscious nervous processes, unless we are able to distinguish between the perceiving *ego* and the *non-ego* perceived (Fichte).

From the objective or physiological point of view (when, that is, we have to judge the existence of conscious states, not in ourselves, but in others), the criterion by which our judgment is guided is founded upon the external signs in which they are expressed. We are sure that an individual has conscious states when he describes the object of his internal experience, and thus shows that he has perceived it clearly. Man is able to express his states of consciousness not only by language but by other external signs, such as mimicry and expressional movements and gestures, and these are the only means we can rely on as evidence of states of consciousness in the higher animals, by the analogy they present with those in which human consciousness is manifested. But as we descend the zoological scale the analogy becomes less reliable, and external manifestations of psychical processes grow increasingly simpler, until finally they lose all value as external signs of true conscious states—at least from the point of view of positive psychology.

As opposed to *conscious*, what we have generically termed *unconscious* is a purely negative idea, to which it is impossible to affix any definite value without an accurate analysis of the different states which it covers.

In the first place, it is impossible to draw a sharp line of separation between the conscious and the unconscious. If we predicate consciousness in a wide sense, that is, as a synonym of

awareness of an object apart from one's self, it may obviously present different degrees between the maximum and minimum of distinctness and lucidity. The threshold of consciousness cannot therefore be symbolised by a line, but is rather a zone which can ideally be divided into different concentric regions like the visual field. Between the *conscious*—symbolically represented by the central area of the retina where colour sensibility is complete—and the *unconscious*—represented by the peripheral zone, where there is total colour-blindness—we can theoretically distinguish other, intermediate regions which express grades of transition between the conscious and the unconscious, and are termed by some neurologists *semi-consciousness, nascent* or *twilight consciousness.*

In these intermediate states the individual has a general notion of psychical experience, a confused sense of objects, but is incapable of projecting them into the external world, and of distinguishing them clearly; he cannot differentiate the self from the not-self as in the fully conscious state.

These phenomena of nascent or twilight consciousness occur normally in the condition of *drowsiness* that precedes sleep, or the half-waking state that precedes waking, in the presence of people talking loudly. The individual who is in this drowsy state may —as many have noticed on themselves—hear the different voices, without being able to distinguish what is said. In the initial or the final phase of sleep, auditory perceptions are confused and indistinct, and almost reduced to the level of crude sensation. Similar in kind is the phenomenon of indistinct and confused vision normal to the achromatic border-zone of the visual field, as described in previous chapters. While there is distinct vision—that is, perfect perception of images—in the central retinal area, in the peripheral zone there is only confused vision—that is, merely a crude sensation of surrounding objects.

These phenomena of semi-consciousness can frequently be observed under a variety of abnormal cerebral conditions, *e.g.* in fainting fits, in chloroform narcosis, in states of sub-coma and stupor, in certain slight epileptic attacks, and so on. These are psychical states in which the field of consciousness becomes so indistinct that the individual is unable to perceive the object of psychical experience clearly, although he is not "unconscious" in the strict sense.

A. Herzen (1879)[1] gives an interesting account of the mental phenomena that develop in *leipothymia* or the last phase of *syncope*, or rather in the subsequent return of consciousness.

"During the syncope there is absolute psychic annihilation, the absence of all consciousness; then at the beginning of coming-

[1] "Trois phases successives du retour à la conscience après une syncope," A. Herzen, *Revue Philosophique*, xxi., 1886.

to, one has at a certain moment a vague, limitless, infinite feeling —a sense of *existence in general* without the least trace of distinction between the *me* and the *not-me*. One is conscious, indeed, of existing, but not of one's organic unity, nor of its limitations. This may be a very agreeable sensation if the syncope is not caused by acute pain, or if one has not hurt one's self in falling, and very disagreeable if there is any cause of suffering. This is the only possible distinction; one feels that one is alive and enjoying, or alive and suffering, but without knowing why one suffers or enjoys, nor what is the seat of this feeling.

"Such is the first phase of returning consciousness—here is the second. Amid the indefinite consciousness of the first phase vague and obscure differences emerge little by little. One begins to see and hear, but the sounds and colours seem to arise within the subject with no idea of their external origin, no link between the various sensations perceived or felt. Each sensation is felt separately, and the whole produces an inexpressible confusion. At this moment the sensory centres have recovered sensibility, but are sensible only of the impressions reaching them directly from without: reflex action is not yet re-established, there is still no combination of sensations into perceptions, and therefore no distinction between the *me* and the *not-me*; in a word, the sensations are *stupid*, if one may so express it, because they are isolated—they can only be felt, and are not known.

"In the next phase, central reflex action is re-established: the various sensations begin to influence one another, to be reciprocally determined, defined, and localised; the several sensory centres unite in the *sensorium commune*, and self-consciousness emerges; but at first it is only an unintelligent feeling, which merely expresses the fact of the organic unity of the subject, and is not a clear notion of the relations with the environment. At this point I felt I was *I*, and that the auditory and visual sensations came from objects that did not form part of me, although I did not yet understand them. The cortical centres, which are the first to suffer, and the last to recover their functional integrity, had not yet recovered.

"Then at a given moment, after the recovery of nutrition, the mind suddenly grasps the situation, and the thought arises, 'Ah, I have fainted again.' From that moment the intellect is completely re-established, and takes the direction from which it had been momentarily diverted by insufficient nutrition."

In this admirable introspective analysis of the gradual recovery of consciousness after its complete suspension in syncope Herzen traces the different phases by which the mental activities pass from total unconsciousness to full consciousness when, as he so happily expresses it, the mind grasps the complex relations of the situation.

It is evident that such a clear and exact description, which amounts to a reconstruction and psycho-physiological interpretation of the several factors, could only be given by a physiologist who was at the same time a psychologist. Its scientific value is therefore a hundredfold greater than all the definitions of "conscious and unconscious," "sensation and perception," formulated by eminent metaphysicians; it is a living page of nascent mental life; it expresses the minute transitions between the extreme mental states, and gives a precise idea of those intermediate states that may as a whole be termed semi-conscious.

It would be interesting to have a similar description of the gradual *abolition* of consciousness, such as must occur on the administration of chloroform for surgical purposes, and of the subsequent gradual return of consciousness. But we have never met with anything relating to this important subject comparable to Herzen's description and of the same value as a control. Any one who has been chloroformed will bear witness to the gradual clouding and final extinction of consciousness, and its subsequent gradual recovery, without being able to differentiate the characteristics of the respective phases.

If we attempt to sum up Herzen's auto-observations into a synthetic formula, it may be said that simple sensations predominate in the state of nascent consciousness, as they certainly do in twilight consciousness, while the true perceptions that we only have in full consciousness are absent. In discussing the physiology of the brain and sense-organs we frequently employed these two expressions, "sensation" and "perception," and endeavoured to differentiate and define them. It is, however, desirable to return to the subject here, so that we may be better able to comprehend this point, which is often neglected by psychologists.

As William James points out, "the words sensation and perception do not carry very definitely discriminated meanings in popular speech, and in psychology also their meanings run into each other." Both terms stand for processes by which external stimuli, acting on the peripheral sense-organs, cause in them an excitation which affects the cerebral centres, and by which we know of the objective world. "The nearer the object cognised comes to being a simple quantity like 'hot,' 'cold,' 'red,' 'noise,' 'pain,' apprehended irrelatively to other things, the more the state of mind approaches pure sensation. The fuller of relations the object is, on the contrary, the more it is something classed, located, measured, compared, assigned to a function, etc., etc., the more unreservedly do we call the state of mind a perception, and the relatively smaller is the part in it which sensation plays. . . . Sensation, then, . . . differs from perception only in the extreme simplicity of its object or content."[1]

[1] *Psychology*, ii. pp. 1-2.

In comparison with Herzen's descriptive definitions those of James appear vague and defective, like all that are the product of pure speculation. According to James, *e.g.*, for adults "a pure sensation is an abstraction" and "pure sensations can only be realised in the earliest days of life." He neglects the absence of distinction between the self and not-self which characterises the sensations that form the content of the first phase of mental life. Not in earliest infancy alone, but in all the states in which intellect is low and feeble, in which attention is weakened and the will ceases to act, the *self* is absorbed in pure sensation; the psychical state loses its lucidity, and becomes a confused and impersonal affective state, with no sharp distinction between the perceiving *me* and the *not-me* perceived.

Pierre Janet, who investigated the lower forms of human psychical activity with much success, expresses the same concept in the following terms:

"Sensation is usually defined as the simple phenomenon which takes place in *me* when *I* see, *I* hear, and so on. But evidently this contains one term in excess, namely, the word *me*, the word *I*. . . . Looking at it from the purely physiological point of view, one is forced to conclude that there are sensations without a self. . . ."

III. When from the phenomena of full consciousness and of semi-conscious states we pass on to examine and define the phenomena generically known as *unconscious*, the ambiguity of this expression is at once obvious. The term may be employed, as Assagioli remarks, either to signify a phenomenon unaccompanied by any state of consciousness (*i.e.* without any character of mentality) or one of which we are not aware (*i.e.* a phenomenon that is unconscious in relation to our empirical or sensorial self, but conscious in relation to the other psychical centre distinct from the self, which is innate in us and forms an integral part of our mentation).

We must thus consider separately two categories of unconscious psycho-physical phenomena: those known by the specific term now accepted by most psychologists as *subconscious*, and those which Morton Prince proposes to term *co-conscious*, or states of *concomitant consciousness*.

In the widest sense the term "subconscious" covers whatever is developed in our mind by obscure processes which are not accessible to introspection. Subconscious phenomena may be regarded as effects of physiological processes of which the self has neither clear, nor confused and obscure, knowledge, in which there is no sharp differentiation between the ego and the non-ego, but which nevertheless form part of our psychical experience. They may coexist and interlock with synchronous conscious processes, or they may precede, interrupt, or succeed them, rising above or

falling below the "psychical diaphragm" that separates the conscious from the unconscious.

"When we examine the actions of other men," writes P. Janet, "we are too prone to credit them with the ideas and arguments that we ourselves employ in interpreting their conduct. Too often we believe that a man has acted with intention, has calculated the consequences of his actions, has formed from his ideas a systematic entity knit together by well-understood relations, while in reality he has allowed his thoughts to run on mechanically, one by one, without grasping any systematic connection between them. . . . Even if the phenomena of consciousness exhibited by any one else appear to us to be interrelated by ties of resemblance, of difference, or of finality, we must not conclude that there was in that man's mind the consciousness of such a resemblance, difference, or finality."

At each moment of our existence our voluntary actions are determined less by conscious motives than by a certain tendency to act in a given manner and a certain repugnance to act otherwise; a tendency and a repugnance for which we are unable to account at the moment of action—that is, of which we only vaguely recognise the motives. At times the hidden impulses to our voluntary acts are in antithesis to the confessed motives which would impel us to act in the contrary manner, if they were not overborne by the secret impulse.

"No one," says Patini (1910), "can be fully conscious at any given moment of the entire range of his field of psychical activity. Part of the psychical processes for ever elude the vigilance of the *ego*. These are the *subconscious*, which consist in motives that are not revealed but remain obscure, although they are strong enough to result in action. In character they are related to actual experience, they become intercalated with our conscious motives, and are essentially active."

This definition is, in our opinion, on the one hand too wide, inasmuch as it confounds *semi-consciousness* with *subconsciousness*; and on the other hand too narrow, because it includes only those subconscious phenomena which are concomitant with conscious manifestations, and apparently excludes from the subconscious those active but hidden psycho-physical processes which precede, interlock with, and succeed the conscious processes. Of these last we have already given some examples to prove that the range of mental life is not confined within the narrow limits of conscious nervous processes, but extends much farther, beyond the extreme threshold of consciousness.

No one has brought out better than Myers, in his strikingly original, posthumous *Human Personality* (1903), the importance of subconscious psychical phenomena—which he terms *subliminal*—in relation to mental life as a whole. On his theory,

the fundamental nucleus and mainspring of human personality is represented by the *subconscious*; the sensorial self is only a fraction of it; from it in large degree we derive our habitual and instinctive tendencies, the impulses to our actions, the spontaneous products of genius.

According to Myers "an 'inspiration of genius' is in truth a *subliminal uprush*, an emergence into the current of ideas which the man is consciously manipulating of other ideas which he has not consciously originated, but which have shaped themselves beyond his will, in profounder regions of his being. There is here no degeneration, but rather a fulfilment of the true norm of man with suggestions of something supernormal, which transcends existing normality as an advanced stage of evolutionary progress transcends an earlier stage. . . ."

"The psychical type to which we have applied the name of genius may be recognised in every region of thought and emotion. In each direction a man's everyday self may be more or less permeable to subliminal impulses. The man who is in but small degree thus permeable, who acts uniformly on supraliminal considerations—on ratiocination, as he will say, and not on impulse—this man is likely to be safe in prudent mediocrity. He subsists upon a part of human nature which has already been thoroughly trained and prepared for this world's work. The man, on the other hand, who is more readily permeable to subliminal uprushes, takes the chance of wider possibilities, and moves through life on a more uncertain way."

In this connection Toulouse (1910) has made an interesting analysis of Henri Poincaré, one of the greatest mathematicians of the age. Poincaré, who was also eminent in physics, astronomy, and philosophy, left an exact account of his methods of work and of the manner in which he reached his important discoveries. It is commonly supposed that researches, conceptions, and constructions of a mathematical character imply the constant intervention of our highest mathematical faculties; Poincaré's introspection, on the contrary, led him to conclude that a subconscious mind works in us, and is active in solving the most difficult problems. He held that thought is constantly permeating the subconscious, and that, as in the semi-waking state, we are never without groups of thoughts of which we are only dimly conscious. When one such thought is particularly new and striking it is drawn into the focus of consciousness and arrested by our reason. According to Poincaré the exact sciences —like poetry and music—owe their progress to the work of this subconscious faculty, and not to our conscious mentation. "What first strikes us," he wrote in *L'invention mathématique* (1908), "are the appearances of sudden illumination, the manifest signs of a long anterior unconscious labour. . . . Often, in working at a

difficult problem, nothing comes off well, at the first attempt; then one takes a longer or shorter rest, and again sits down at the table. Again for the first half-hour nothing occurs, and then suddenly the determining idea crops up in the mind. . . . This pause has been filled by an unconscious travail."

He gives a characteristic description of the way in which he discovered the Fuchsian functions by which so many algebraic equations have been marvellously simplified. "For a fortnight I had been trying to prove that no function, analogous to what I have since termed the Fuchsian functions, could exist. I was then very ignorant. I sat down every day at my writing-table and remained for an hour or two; I tried a vast number of combinations and failed to reach any result. One night, contrary to custom, I drank black coffee and could not sleep; my thoughts came crowding up; I felt them tumbling over each other till two became as it were locked together so as to form a stable combination. In the morning I had established the existence of a class of Fuchsian functions . . . it only remained to tabulate the results."

Some physiologists and psychologists have objected that Myers' theory is exaggerated, but the observations of Poincaré seem to afford a direct proof of it. Del Greco (1906) made many criticisms, with a view to emphasising the supreme importance, in the collective mental activities, of the *supraliminal self*. But he has overlooked the fact that Myers foresaw this criticism and opposed to it the following statement:

"I do not mean to imply that subliminal is *ipso facto* superior to supraliminal mentation, or even that it covers a large proportion of practically useful human achievement. When I say 'the differentia of genius lies in an increased control over subliminal mentation,' I express, I think, a well-evidenced thesis, and I suggest an important inference, namely, that the man of genius is for us the best type of the normal man, in so far as he effects a successful co-operation of an unusually large number of elements of his personality—reaching a stage of integration slightly in advance of our own. . . . That which extends *beneath* the threshold, *beyond* the margin of a field of consciousness specialised for our ordinary needs, will probably be both more extensive and more miscellaneous than that which is contained within those limits. . . ." Genius, he continues, is no aberration of the human mind, no sign of its degeneration; in the evolutionary scale genius forms by no means either an extreme term or an accidental deviation. The higher gifts of genius—poetry, the plastic arts, music, philosophy, pure mathematics—which are often called *by-products*, because they have no manifest tendency to aid their possessor in the struggle for existence in a material world, are all perceptions of new truth and powers of new action decisively predestined for the race of man.

These statements by the most courageous and convinced of the English spiritualists are substantially confirmed by the most cautious of the French positivists, Th. Ribot. "It is the unconscious," he writes, "that produces what is vulgarly termed inspiration. This state is a positive fact, presenting specific physical and psychical characters. Above all, it is impersonal and involuntary, acting after the fashion of an instinct, when and how it will; it may be entreated, but it suffers no constraint. Neither reflection nor will replace it in the original creation. The eccentric habits which artists indulge in during their creative periods merely tend to create a special physiological condition, and to increase the cerebral circulation so as to arouse or maintain unconscious activity."

The only objection that can be made, either to Myers or to Ribot, is that their psychological theory combines into a single category (the *subliminal*, or the *unconscious*) two distinct forms of mental activity; that which many now term "subconscious," *i.e.* (on the definition we have accepted) whatever operates and develops within us in a manner that is hidden or removed from introspection, and that which we are about to examine under the definition of "co-consciousness"—the *secondary personality* of psychiatrists, or *subliminal ego* proper.

IV. A much-disputed question among physiologists and psychologists is whether the subconscious is based upon processes that are purely physical or material, or upon psycho-physical processes, like conscious phenomena. Can we, or can we not, admit a psychical activity in which there is absolutely no mentality, *i.e.* which consists in purely physiological processes? Can it be assumed that certain normal or pathological states of the nervous system, such as sleep, coma, epileptic states, etc., represent genuine interruptions of the mental processes; or are the latter, while they vary considerably in vigour and distinctness, never absolutely interrupted during life?

Carpenter was the first to support the former proposition under the somewhat clumsy name of "*unconscious cerebration*," which was then adopted by reliable psychologists like Münsterberg and Ribot, and the American psychiatrist Morton Prince. The latter view is held by most physiologists and psychologists, particularly by those who, to represent the mysterious relation between mind and body, adopt the pragmatical hypothesis of psycho-physical parallelism, which they extend to all specific vital processes, or at least to those of the nervous system, and particularly to that part of it which subserves the functions of animal life.

This is a very difficult question, and from the standpoint of positive science, no exact solution, free from ambiguity and uncertainty, seems possible.

Every one will allow that our psychical capacity and inherited cognitions develop and grow and increase progressively, in consequence of the gradual and methodical exercise of our mental powers. Every psychical experience, each new perception and thought, leave a record in the mind, by adding to our inherited memories, altering our affectivity, developing our habits, and forming our tendencies. If we want to express these changes and integrations, of the nature of which we are totally ignorant, in terms of physiology, that is of external observation, we say that every psychical experience leaves a material trace in the higher nerve-centres, facilitates the conduction of the impulses along given neural paths, creates, or at least opens up, new associative ways between the different centres which are involved in the manifold and complex psychical processes. If, on the contrary, we want to express the same fact in psychological terms, *i.e.* of introspection, we say that each new psychical experience is a transitory phenomenon in relation to self, but persistent and continuous in relation to the deeper and hidden regions of our mind—which are constantly active, even when this activity drops below the threshold into the subconscious.

Neither the one nor the other interpretation of the development and integration of the mind gives a true scientific explanation of it: they merely offer a working concept or hypothesis, with no objective value, and are wholly inadequate to explain the mysterious relation that exists between the mind and the nervous system. This is evident, as Assagioli points out, from the severe criticism of methods and scientific postulates made by the most modern scientific philosophers, especially Pearson, Clerk-Maxwell, Ostwald, Mach, Le Roy, Poincaré.

In favour of the psychological interpretation it should nevertheless be noted that the subconscious as a psychical activity entirely divested of consciousness is inconceivable, and that there are other facts which appear to confute the thesis of unconscious cerebration, with its corollary of the absolutely unconscious in vital phenomena. Some of the arguments based on these facts have been well brought out by William James.

In speaking of *sleep*, we saw that it is often accompanied by *dreams*, which are in themselves an imperfect form of mental activity, because when suddenly awakened during sleep we may be vaguely, sometimes definitely, aware that we had been dreaming. During somnambulance and in hypnosis a considerable amount of mental activity can be displayed, but all trace of this activity is obliterated on waking.

Both in the waking state and in conversation, ideas and images often crop up in the mind which are instantaneously effaced, and cannot be reinvoked, making an unpleasant break in the thread of our reasoning. This shows that even during the

conscious workings of the mind the subconscious is active, although every trace of its activity may be instantaneously blotted out from introspection owing, as Myers would say, to the varying permeability of the "psychical diaphragm" which separates the conscious from the unconscious.

It is further interesting to note that the peripheral sense-organs are pervious to ordinary excitations not only in the waking state but also in sleep; although we may pay no attention to the impressions they send to the central nervous system if our judgment pronounces them not to be worth attending to. Some people are in the habit of sleeping, and sleeping profoundly, in the midst of noises, as though these were unable to excite the auditory centres during sleep. This, however, is not the case. As James observes, the mother, sleeping amid far stronger noises, awakes the moment the child stirs; and the same is true of a nurse and patient. This proves that in sleep, independently of consciousness, the auditory centres are not only excited by external sounds, but the mind is also capable of differentiating them and judging of their psychical value.

Another more commonplace argument put forward by Vaschide to show that unknown to the sleeper the mind is active during sleep is the striking capacity many people possess of knowing the time and measuring its passage in their sleep. They are able to wake up every day at the same moment, and even in some cases at an unusual hour decided on prior to sleeping. This is inexplicable unless we assume an activity of the mind during the entire period in which sensorial consciousness is completely suspended.

Other arguments to the same effect have been adduced by James from certain curious phenomena observed in hysterical subjects, and proved by Pierre Janet (1889) and Binet (1890) not to be due to deception.

If we admit the psycho-physical nature of subconscious processes it is evident that they are the continuation of past mental experiences, and are fundamentally derived from the anterior history of the *ego*. In all probability, as we have said, the conscious psycho-physical processes are not extinguished, but persist even when they become subconscious. Every representation and idea has, as maintained by Gross (1902), a *primary* function at the moment in which it occupies consciousness, and a *secondary* function by which it acts in the succeeding moments, and influences the whole of the psychical current, either by facilitating or by obstructing its course. This secondary function comes into play when the consciousness is occupied by other ideas, so that it is either perceived in a vague, confused manner, or not at all. In the first case it enters into the semiconscious, in the second into the subconscious field.

It seems probable (if we may be permitted for a moment to pass the bounds of positive knowledge) that subconscious psycho-physical processes play over the whole of the vast area of the living world. There is nothing unreasonable in the idea that all the complex functions by which living organisms—plants and animals—are differentiated from the inorganic aggregates of non-living Nature are accompanied by, or have the character of, subconscious psycho-physical processes. The sensibility of plants, admitted even by the older botanists, must not be interpreted in a metaphorical sense as a mere increase of excitability, but in a true psychological sense as the capacity of feeling elementary sensations, from which subconscious states arise. In all plants—as Tangl first observed in germinating seeds—the living elements, from the simplest cellular groups to the most complex of the higher vegetables, are connected by the protoplasmic filaments, or *plasmodesmata*—which recall the fibrils of the animal nervous system. By means of this elaborate system of protoplasmic filaments some plants are capable of responsive and protective acts, similar to those observed when the lower animals react to external stimuli. This capacity for reaction is for the most part diffused throughout the vegetable protoplasm; in other cases it is localised more particularly in certain parts (leaves, roots); in others again in special organs, which by their peculiar structure recall the sense-organs of animals—as was pointed out by Noll (1896), and described in more detail by G. Haberlandt and Nemec (1900).

In many, especially among the higher plants, special organs have been recognised morphologically and experimentally that are able to react to mechanical stimuli, like the tactile organs of animals; special organs on which depend the positive geotaxis of the roots, the negative geotaxis of the stems, the transverse geotaxis of the leaves, similar to the organs of orientation in animals; lastly, special organs adapted to react to the light stimulus, on which heliotaxis depends, and which by their complicated structure recall the visual organs of animals.

Granting all this, it seems to us—without admitting the exaggerated pretensions of Haberlandt—that it is not unreasonable to admit that plants exhibit rudimentary phenomena of psychical life; in other words, that the various forms of sensibility in vegetables are the expression of specific psycho-physical properties inherent in the complex structure of living protoplasm. But remembering that plants, like the lower animals, are destitute of central organs homologous to the nervous system of the higher animals, there can be no doubt that they have no conscious subjective phenomena; *i.e.* that in them, as in the lower animals, all forms of association and of psychical synthesis, on which the multiple and graduated forms of conscious life depend, are absent.

We may conclude that the unconscious extends into the lower

forms of life, as the germ or immediate potentiality of the conscious, which develops in the higher animals and in man by a process of evolution. The subconscious in plants and metazoa is the same as that specific activity of living beings which Aristotle and Leibniz termed *entelechia*.

Admitting the credibility of this hypothesis it follows logically that in the higher animals and man, with elaborate nervous systems, the region of the unconscious is not confined to the organs of animal life, but extends beyond it to embrace the vegetative organs.

V. The segmental theory founded by Moquin-Tandon (1827) and Duget (1837), according to which animals, generally speaking, result from a series of complex morphological aggregates (the *zoönites* of invertebrates, *metameres* of vertebrates), each of which represents in miniature the organisation of the animal to which it belongs, has been much developed, and has acquired a general biological importance.

The foundations of a segmental anatomy are already laid. We know that the skeletal system and muscles, the nervous system, and the skin of vertebrates exhibit in early developmental stages or throughout life, in certain parts or in the whole organism, a more or less obvious division into segments of the same kind arranged in series. This is shown by a mass of different researches of various kinds, of which van Rynberk published a bibliography in 1908, which are the foundation-stones of a segmental physiology, or the arrangement of functions according to their uni- or pluri-segmental localisation. Van Rynberk has indicated this in a recent memoir (1912).

The most interesting fact from our point of view is that in proportion as we ascend the zoological scale the *unitary* or *monozoic* constitution gradually replaces the *segmental* or *polyzoic*, owing to the increasing interpenetration and fusion of the component segments. The *zoönites* of invertebrates, which represent an almost independent individuality, become *metameres* in vertebrates, which while they have the same biological significance are closely interconnected. From Amphioxus to Man, metamerisation, which is obvious during embryonic development, becomes more and more masked during development, while the centralisation—effected particularly by the nervous system—is increasingly emphasised in the higher animals.

Man, at the summit of the scale, presents the most complicated constitution, and is at the same time the most profoundly unitary of all living beings: this is evident in the phenomena of the self or sense of personality, which maintains a steady and apparently invariable attitude in face of the incessant stream of thoughts, feelings, and actions.

Nevertheless, the self, as already pointed out, comprises only a

fraction of the phenomena of mental life, our personality is no *monad*, no indivisible entity; the centralisation of the metameres from which the brain was originally derived is—while almost complete from the anatomical point of view—exceedingly imperfect from the physiological standpoint, as is proved by the modern doctrine of cerebral localisation.

Further, the evidence of disintegration or fragmentation of personality, as the double consciousness observed in hysterical subjects, in which the primary person or supraliminal self is associated or alternates with a secondary person or subliminal self, along with other strange phenomena well established by psychiatry, experimental hypnosis, and occultism, may be taken as the first indications, if not as direct evidence, of a possible or at least conceivable *segmental psychology*. These phenomena are not capable of strict scientific analysis, and they baffle the philosopher by their great complexity, leaving him to flounder in the unexplored abysses of human nature. Yet the physiologist and psychologist must not spurn this study with the specious and futile argument that we are not yet in a position to reconcile it with those common postulates of physical and biological science which have been accepted as intangible dogmas. Taken as a whole, these abnormal phenomena (subnormal or supranormal), whether spontaneous or provoked, are equivalent to vivisection experiments upon the human mind. As such, they are valuable in psychological analysis, because normal phenomena, owing to mental exaltation or dissociation, assume undue proportions, which facilitates the study of the individual elements or components of the human intellect.

We must not trespass on the field of psychiatry by entering too closely into these phenomena. It is enough to draw attention to one of the simplest and clearest instances of *double consciousness*, namely that known as "automatic writing." Certain individuals, from congenital or acquired predisposition, strengthened by practice, are able to detach part of the complex psychical activities which build up their personality, and to emphasise and develop the subconscious functions into a secondary self, entirely separate from the primary self, which thus by automatic writing reveals a psychical phenomenology which is often senseless and stupid, but may be coherent, logical, and tolerably well developed. These are the phenomena which Morton Prince terms "co-conscious," as they coexist with the conscious phenomena of the primary personality. The latter may be fully awake and engaged in conversation or otherwise, while the secondary personality expresses itself mechanically in writing.

More curious, but equally authentic, are the cases of *alternating personality*, in which the primary self is replaced by a secondary self, or the reverse, in successive and more or less extended periods. Invariably in these cases of alternating personality, as

in the well-known instance of Felida X described by Azam (1876), the primary self has no knowledge of the secondary, nor the latter of the former. The two personalities that alternate are wholly separate as regards memory. Personality A is incapable of recalling what took place during the period in which personality B was active, and *vice versa*; the two personalities mutually ignore each other, as if separated by an impermeable diaphragm. As we have seen, no such impermeability exists between conscious and subconscious activity, the supraliminal and subliminal self of Myers. At each moment of life our thoughts and actions are not only determined by external sensations and conscious motives, but are largely influenced also by obscure internal sensations and subconscious motives, which are generically known as tendencies or instincts. There is a constant interplay between the subconscious and conscious activities, and the mind—that is, our psychical personality as a whole—results from the continuous co-ordinated collaboration of the conscious with the subconscious.

However mysterious from the scientific point of view may be the process which makes possible the disintegration of the human mind into two distinct consciousnesses, coexistent or successive, we can nevertheless state that it results from two factors: abnormal dissociation of conscious from subconscious psycho-physical processes, and abnormal functional exaltation of the latter, or, better, of a portion of them, into a new conscious psychical entity, *i.e.* a new and distinct personality or *subliminal ego*. Probably the two factors stand in the reciprocal relation of cause and effect: it can readily be imagined that dissociation promotes exaltation, while, conversely, exaltation promotes or determines the functional dissociation of the two portions of the mind.

P. Janet believed that disintegration of human personality could only occur in states of nervous enfeeblement, as in hysterics who exhibit an imperfect unification and co-ordination of the mental functions. Owing to this psycho-asthenia, hysterical subjects are incapable of holding their personality aggregated in an organic whole, and they consequently lose control of the secondary personality.

Experience does not, however, justify this limitation of the phenomena of dissociated personality merely to pathological conditions, particularly to hysteria. Janet himself has recently changed his opinion, and admits the possibility of the existence of the co-conscious in normal individuals. This, which he admits as *possible* only, seems on the strength of a number of arguments to be also *probable*.

In every human being, even under perfectly normal conditions, there is a more or less pronounced differentiation, sometimes an

opposition between the conscious reasoning self and the subconscious self, expressed in the form of vague sentiments which form our instinctive tendencies and impulses. To this want of harmony between the conscious and the subconscious we must refer the inequalities and incongruities of character and conduct which are emphasised in persons to whom we apply the epithets of unbalanced, eccentric, or mad.

It cannot have escaped the attention of teachers and moralists that these incongruities and irregularities in character and conduct are most striking during the period of development, when the functional activity of the brain is incomplete; they are less prominent in adult life, when the nervous system has become finally adjusted, and the passions of youth have calmed down; but they sometimes reappear in old age, when senile degeneration of the nervous system sets in. This shows that the incongruities and irregularities of character depend on incomplete fusion and functional co-ordination of the hypothetical segments that build up personality; in other words, they point to the possibility of a disintegration of consciousness.

A still more definite indication of dissociated personality in normal subjects, independent of their age, is described by William James in the "sense of presence" that is often felt by people endowed with a mystical, religious temperament. All the good actions and works of charity which they perform are inspired by a good genius, a guardian angel who is always present in the depths of their personality; all the selfish and passionate acts, all the sins they commit, are due to the suggestions of a bad genius, a tempter of whom they are aware in the darker, more atavistic regions of their soul. In mystics—no matter what dogmatic religion they profess—the "conscious" and the "subconscious" are not really fused together into a single individual; the suggestions of the subconscious are perceived introspectively as the product not of intrinsic causes or conditions, but of causes or agents extrinsic to their own individuality. To complete the doubling or disintegration of personality in a mystic, two further factors alone are necessary—the diaphragm that, in Myers' picturesque metaphor, separates the conscious from the unconscious, must become impermeable, and, in consequence of this complete functional separation of the two portions of the mind, the activity of the subconscious must be exalted till it becomes a co-conscious psychical entity.

Not altogether without reason, biologists and psychologists in general have refused to recognise any very high order of intellect in mystics. Often, indeed, as the critical spirit develops and scientific culture spreads, the religious spirit cools and the halo of mysticism disperses. "As science advances, God withdraws," is the audacious dictum of Proudhon. We must, however, abstain

from generalisations; a right distinction must be made between the mysticism founded on the beliefs and superstitious practices that underlie all positive religions, and the noble mysticism of spiritually and ideally minded philosophic thinkers. Reverence is due to the great mystical personalities of whom ancient and modern history give us classical examples, such as Socrates, moralist, martyr of philosophy, and splendid personification of human dignity. The legend that Socrates was or believed himself to be inspired by a daemon or familiar genius has been constantly repeated since the time of Plato; but there is no direct evidence to show that he suffered from auditory or visual hallucinations, or that he imagined that he held converse with a spirit, as was too hastily assumed by Lélut and Moreau de Tour. Modern critics have refuted this statement, as Morselli has well brought out in a synthetic review of the question (1882).

D'Eichthal, who made a profound study of the *Memorabilia* of Xenophon, the most direct and faithful disciple of Socrates, states that in every place in which the celebrated word δαιμόνιον occurs, it has the meaning of θεός, like the word δαίμων in Homer; while the δαίμονες of Hesiod are genii intermediate between man and the divinity. The word δαιμόνιον is a neologism created by Socrates, and not met with in any other Greek author before Xenophon. Fouillée holds that Socrates intended it to signify the analogy between his internal monitions, inspired by the divinity, and the daemons of Greek mythology. This interpretation is too metaphysical. It is, however, certain that in Xenophon there is no trace of the "demons" of popular superstition. According to d'Eichthal the true creator of daemonology was Plato, who perhaps interpreted his master (who, as we know, left no written records and always taught by word of mouth) more liberally and less faithfully than Xenophon. None the less it seems to us reasonable to suppose with Hild that Socrates—though a monotheist—believed in the existence of genii intermediate between man and divinity, and that the legend of the "familiar daemon" which inspired him had some foundation in reality.

What then are those daemonic monitions claimed by Socrates (and admitted also by Schleiermacher, Cousin, R. Bonghi, Decharme, Renouvier, Zeller, and others) if not the suggestions of the subconscious, which in all mystics assume a special activity presented to introspection under the form of a phantasm, an extrinsic individuality, of which they are continually aware in the recesses of their soul?

To us there seems no doubt that the familiar spirit which inspired Socrates, who was proclaimed by the Oracle of Delphi the wisest of men, indicates that in each normal individual in whom the subconscious reaches a high degree of activity, as in

the mystics, in saints, and in men of genius generally, there is an imperfect unification of the psychic personality, and more or less manifest evidence of the existence of a secondary personality, that is a *subliminal ego.*

VI. The alternate sequence of waking and sleep bears some resemblance—at least in its first origin—to the succession of day and night.

The rhythm of activity and rest, of functional energy and torpor, of mobility and quiescence, of waking and sleep, can be observed not only in man and in most animals, but also in plants, according to early observations of Clusius, Prosperus Alpinus, and Linnaeus. In many plants, in fact, the leaves and flowers expand during the day and shrink or fold up at night. A number of botanists have studied this phenomenon experimentally, and ascribe it to the diurnal and nocturnal variations of meteorological, electrical, and hygrometrical conditions, to the influence of light and heat, etc. They deny that the sleep of plants is similar to that of animals, and reject the teleological motive of protection from nocturnal cold and of rest, ascribed to them by the earlier observers. In a recent monograph on the *Physiological Problem of Sleep* (1913) Piéron maintains that sleep—understood as a suspension of the sensori-motor activities that bring the living being into relation with its environment—is not an absolute necessity. The so-called sleep of plants only presents a superficial analogy with the slumber of the higher animals. On the other hand, it is impossible to discover evidence of sleep in many vertebrates.

Still, in view of the incontestable biological analogy between animal and plant protoplasm, the susceptibility of both to anaesthetics, and particularly the existence of rudimentary sense-organs in plants, it may legitimately be claimed that the rhythmical oscillation of the functional activity of organs—which in the higher vertebrates takes the form of waking and sleeping—is a universal phenomenon, originally associated with the physical changes of the atmospheric environment, and recurring rhythmically with day and night.

"The time of rest is night-time," writes Rousseau; "it is marked by Nature. It is a matter of constant observation that sleep is quieter and more placid when the sun is below the horizon." Daylight sleep, in fact, is less recuperative and less profound and unbroken than night sleep. The depression of reflex activity, slowing of the pulse and respiration, fall in thermogenesis, etc., are less pronounced in sleep by day than by night (Vaschide, 1906). Darkness and silence are favourable to sleep by day, which attains its maximum more slowly, and has an irregular curve; its onset is more sudden and its awakening more rapid; its dreams are more logical, its oniric current more reasonable,

its memory of dreams on awakening more vivid. Everything, in fact, goes to show that sleep by day is lighter than by night, and that Nature—as Virgil says—made the alternations of sleep and waking to coincide with those of night and day.

When we feel the need of sleep, we seek a convenient posture, in which muscular relaxation is most complete. In consequence of habit this need makes itself felt every day at the same hour. But darkness, silence, or a monotonous sound, the incessant shaking of a train, a dull lecture, the state of digestion, mental fatigue, and lastly ennui and distaste for one's surroundings, all induce sleep, and make the want of it felt even at unaccustomed hours.

Sleep is usually preceded by a sensation of pricking in the conjunctiva and the cornea, due to dryness from the cessation of the lachrymal flow, by yawning, heaviness in the head, weariness in the limbs, closing of the eyelids, asynergy of the conjugated movements of the eyes, difficulty of focussing attention, and finally by progressive dulling of the senses. In the state of *drowsiness* that precedes sleep there is a sort of rhythm in psychical activity, expressed in alternate concentration and distraction. The former becomes shorter, the latter longer, till consciousness is suspended. The initial *hypnagogic hallucinations* coincide with the states of distraction or vacancy: they are usually visual, like those described by Cardano, Goethe, and Joh. Müller, and become more and more vague, disconnected, and void of sensorial elements, till they finally merge into a state of absolute vacancy or unconsciousness. Sleep supervenes in one of these states of hallucinatory distraction, which lasts barely 2-3 or at most 5 minutes.

The same rhythm of alternate states of attention and distraction occurs in the drowsiness that precedes awakening. Attention is at first very transient and then becomes more concentrated, at the expense of the states of vacancy which are gradually emptied of hypnagogic illusions. Awakening occurs at the moment when this mental rhythm tends to disappear in the normal course of the psychical process of waking up (Vaschide and Vurpas).

The duration of sleep varies with many extrinsic and intrinsic conditions. New-born infants sleep 18-20 hours of the day; adults on an average 8 hours; old people only 5-6 hours. Women usually sleep more than men. Convalescents sleep a great deal after acute illnesses, and this also occurs at the beginning of grave illness (Doublé). The influence of climate, as the effect of hot and cold seasons, is uncertain.

The depth of sleep varies from its commencement to its close. Kohlschütter (1862) first attempted to measure and construct its curve at Fechner's suggestion. He employed auditory stimuli, on

the assumption that the sound necessary to arouse the sleeper must be in direct relation to the profoundness of sleep. This research was repeated by Mönninghoff and Piesbergen, Michelson, Römer, and Weygand. They distinguished a *normal type* of sleep, which reaches its maximum after about an hour, then becomes gradually less profound, and finally rises again towards morning, from an *abnormal, neurasthenic type*, which reaches its maximum later and decreases more slowly. As regards the value of these researches De Sanctis pointed out that sleep is not equally susceptible to auditory stimuli in all subjects, and that sleep of the auditory sense is not coextensive with general sleep.

Waking is usually a spontaneous or automatic act, but may also be determined and provoked. This occurs either because we have slept enough, after the habitual eight hours of repose, or because a sudden external stimulus or certain internal sensations (hunger, thirst, cold, and those due to an uncomfortable posture, or the desire to micturate, or the emotion produced by certain dreams) interrupt sleep, or because we have previously determined to wake at a certain hour. Many people succeed in waking approximately at the hour they decide on, and are never more than fifteen minutes out.

Tschisch, in methodical researches on prearranged waking, found that he invariably awoke before the hour decided on—never later. Vaschide's investigations showed that sleep under these conditions (*sommeil expectatif*) differs from ordinary sleep; it is more restless, and troubled by curious dreams. We have already discussed the psychology of prearranged waking (p. 453).

The psychical phenomena of waking are not fundamentally different from those of nascent consciousness after syncope, described by Herzen (*supra*, p. 444). The gradual passage from sleep to waking was aptly defined by Buffon as "a second birth." In the briefest possible time we recapitulate all the phases of the psychical development of the new-born infant and the babe.

The activities of the organs of vegetative life are not suspended during sleep; *somnus labor visceribus—motus in somno intra vergunt*, wrote Hippocrates. It is worthy of note that while the chemical processes of digestion proceed actively, the intestinal movements and peristalsis are diminished. Digestion, particularly after an abundant meal, usually produces drowsiness, due, some say, to the congested state of the abdominal viscera which produces a corresponding ischaemia of the brain. On post-mortem examination of persons who died in the night the food is found more digested in proportion to the time that has elapsed since the last meal—which sometimes affords medical evidence as to the hour of a violent death. Assimilation during sleep appears to be favoured by the resting state of all the organs of animal life.

Much sleep, in fact, induces plumpness, while wakefulness tends to emaciation.

Volkow (1900) described the sleep of inanition in the *liojka*, or winter fast of the poor mujiks on the Russian steppes, who lie silent in bed for the greater part of the cold season. This is not, however, a physiological sleep, but a *hibernation*, similar to that of marmots and hibernating animals in general.

Secretions, generally speaking, diminish during sleep. The lachrymal secretion begins to decrease, as we have said, when drowsiness sets in. The salivary and mucous secretions also diminish, as proved by the common fact that the mouth and nostrils become dry in sleep.

The secretion of urine diminishes in sleep, and has consequently a higher specific gravity in the morning than during the day. Urine secreted by night produces convulsions, that secreted by day has a narcotic effect when injected into animals (Bouchard).

Cutaneous perspiration, on the other hand, increases during sleep. Santorio affirms that a man perspires as freely in seven hours of sleep as in fourteen when awake.

The respiratory rate is slower during sleep, and may become intermittent or even periodic, especially in children and old people (Mosso, Luciani); the inspiratory movements of the diaphragm almost disappear, so that the *abdominal* type becomes *costal* during sleep. Each inspiration is longer, and the expiration shorter.

The output of carbonic acid is considerably diminished during sleep (Pettenkofer and Voit), owing particularly to the inactivity of the muscles; while the oxygen absorbed is partially stored up in the blood and tissues.

The beats of the heart slow down during sleep; *pulsus in somno parvi, languidi, rari,* wrote Galen. But the action of the heart is not uniform throughout the whole period of sleep; it increases as the moment of waking draws near (Doublé). A fall in arterial pressure has also been noted during the first five hours of sleep, followed by a rise up to the moment of waking (François-Franck, 1881; Brusch and Fayerweather, 1901). In general, the tone of the involuntary muscles of the intestines, bladder, etc., is depressed during sleep (Mosso, Pelacani, and others).

The peripheral vessels are congested during sleep owing to the slowing of the circulation and the diminished tone of their walls (Mosso, François-Franck). This effect increases up to the second hour of sleep, and then decreases to the moment of awakening (Howell, Lehmann).

The study of sphygmograph and plethysmograph tracings taken during sleep shows periods of automatic constriction and dilatation of the blood-vessels. Sensory stimulation during sleep produces quite different vasomotor effects from those that result

during waking (Mosso, Vaschide and Vurpas). Fano (1885), and Rummo and Ferannini (1888), noted an appreciable delay in the vascular reflexes during sleep, that is, the vasomotor reaction time is increased.

The fall in body-temperature during sleep was known to Hippocrates. But Haller correctly points out that in regard to thermogenesis we must distinguish between physiological sleep and that induced by narcotics. The thermometric observations by Marie de Manaceine show that in sleep the axillary temperature drops in summer to 36·45 C., in winter to 36·05 ; it is lowest between midnight and 3 A.M. This nocturnal fall of temperature is due to diminished katabolism and therefore to reduced thermogenesis during sleep.

All these functional changes in the organs and systems of vegetative life correspond to the depression of the metabolic activities of the sleeping organism, or more exactly to a predominance of the anabolic or assimilative over the katabolic or dissimilative processes.

The changes in the organs of animal life during sleep are more characteristic.

In slumber we lose the use of our senses, but they do not all fall asleep at the same time, nor do they all sleep in the same degree. The "sleep" to touch is light, while gustatory and olfactory stimuli take effect with more difficulty. Hearing, like touch, is excited in most sleepers by slight stimulation : it is the last sense to succumb, whereas sight is the first that passes into abeyance. The closure of the lids during sleep is due to fatigue of the levator palpebrae muscles. The eyeballs are directed upward and diverge, the pupils contract and dilate at the moment of waking—a *myosis* and *mydriasis* due to decrease or increase in the tone of the vaso-constrictor nerves of the iris, rather than to relaxation or spasm of their antagonist muscles (Gubler and Langler).

The diminution of sensibility, or sleep of the senses in general, is due to inactivity of the cortical centres rather than to alterations in the peripheral sense-organs. The latter, in fact, are pervious to stimuli during sleep ; they may react to sounds or noises, to light even through closed eyelids, and to contacts and odours even in slumber. During sleep the excitability of the cerebral cortex to experimental stimuli diminishes (Tarchanoff, 1894), as well as the tendon and cremasteric reflexes (Rosenbach, 1879), the vascular reflexes (Patrizi, 1896), and the pupil reflexes (Berger and Loewy, 1898).

The voluntary muscles are relaxed in physiological sleep, yet they often carry out co-ordinated reflex movements, initiated by tactile or painful sensations, as the sting of an insect, or a cramped position, etc. Again, apart from somnambulism, which is an

abnormal state, there are well-known instances of men sleeping on horseback, and soldiers falling asleep on a long night-march. Galen relates that in a night's journey he slept through an entire stage. These curious instances are explicable on the theory of *partial sleep*, which invades all centres except those on which the automatic activity of the locomotor muscles depends.

To sum up, therefore, and define the characteristic features of sleep, apart from all the concomitant factors, such as diminution of sensorial excitation due to the quiet of night, reduction of mental and muscular activity, and the horizontal posture, it may be said to consist specially in variations of the cardio-vascular, the respiratory, and, above all, the sensori-motor activities.

VII. The complex physiological phenomena of sleep, as set out above, prove clearly that it is not confined to the brain, but involves the entire organism more or less. Nevertheless, the most characteristic feature of sleep is the resulting state of the nervous system, which has led many to regard the brain as the part most implicated.

The principal hypotheses put forward to explain the genesis and nature of sleep are based on the changes that can be observed in the functional activity of the brain in waking and sleeping. These must be examined not so much for their intrinsic value as for the experimental researches made in connection with them.

The earliest were the *circulatory theories* of sleep. Observations on the cerebral vessels during sleep are contradictory: some authors described an ischaemia, others a cerebral hyperaemia. Blumenthal (1795) was the first who stated that sleep is associated with contraction of the cerebral vessels, from his observations on the exposed brain of a boy with a cranial fracture. Donders, Kussmaul and Tenner, Durham, Hammond, Cl. Bernard, and others held the same opinion, after trephining the skull in animals. Salathé (1877) gave the same interpretation to his observations on the movements of the fontanelles in infants.

Mosso, Howell, and Lehmann made observations with the graphic method on certain subjects with cranial defects, and saw that changes in the cerebral circulation could be observed even in the period of drowsiness that precedes slumber: the sphygmograms were lower and more uniform in proportion as sleep became more profound. While the vessels of the forearm dilated during sleep, those of the brain contracted. Stimulation of any peripheral sense-organs during the waking state sufficed to produce a rise in the cerebral pulsations and a simultaneous fall in those of the forearm. The same antagonistic effects were produced during sleep, even when the stimulation was not strong enough to cause awakening. During gradual awakening dilatation of the vessels and increase of brain volume was observed, while the vessels of the forearm contracted; in sudden awakening by strong

external stimuli, the dilatation of the cerebral vessels was, on the contrary, preceded by a brief period of vascular contraction.

Other authors have adduced diametrically opposite observations: during sleep they noted hyperaemia and cerebral vaso-dilatation, instead of ischaemia and vaso-constriction.

Czerny (1891) saw, in a boy who had a traumatic defect in the skull, that when the patient closed his eyes and respiration assumed the characteristic type for slumber, the height of the cerebral pulsations increased, and attained its maximum in the first half-hour of sleep, *i.e.* in the deepest phase.

Brodmann (1902), by plethysmograph researches on a patient trephined in the occipital region, stated that slumber was characterised by a marked increase, awakening by a diminution, in the volume of the brain. He contradicted the observations of Howell and Lehmann and of Mosso, and demonstrated that neither in sleeping nor waking was there any antagonism between the cerebral circulation and that of the forearm.

It is not easy to account for the contradictory character of these results. For the theory of sleep it suffices to point out that cerebral hyperaemia or anaemia are accessory phenomena, and not the main factors on which sleep depends, since it supervenes independently of the state of the cerebral circulation. Vulpian observed that faradisation of the upper segments of the two cervical sympathetic trunks does not produce general sleep, although it induces a certain amount of cerebral ischaemia. On the other hand, Brown-Séquard showed that bilateral section of the cervical sympathetic, which is followed by cerebral vaso-dilatation, does not perceptibly disturb the rhythmic recurrence of sleep.

Charles Richet adduced several arguments in support of the view that sleep is independent of changes in the cerebral circulation. Sleep is almost universal in living beings; the alterations in the cerebral circulation in sleep or waking are not so great as those due to simple variations in the position of the head; even decerebrated pigeons exhibit alternate periods of sleep and waking after a few days, as did also the brainless dog of Goltz.

Everything therefore speaks in favour of the view that the depression of cerebral functions, which is the culminating phenomenon of sleep, depends on a change of unknown character in the nerve-elements of the brain, and that the changes in the central circulation are only collateral secondary phenomena.

One of the facts best ascertained and admitted by every one is the beneficent and restorative action of sleep on the organism as a whole, particularly on the psycho-physical functions of the brain and nervous system in general. Hippocrates, Aristotle, and Galen had already noted the deleterious effect of prolonged waking. Bacon regarded sleep as an essential condition of the prolonging of life.

Certain facts indicate that sleep is more necessary than food. It is possible to fast four to five weeks, but enforced deprivation of sleep kills in a few days. Montaigne relates how Perseus, king of Macedonia, a prisoner in Rome, was done to death by want of sleep. And there are well-attested facts from experiments on animals which illustrate the fatal effects of enforced wakefulness. Bordoni-Uffreduzzi cites the case of three healthy boys who vowed that they would not sleep for a week, and resorted to various ways of keeping themselves awake. One of them on the fourth day fell asleep suddenly after a gymnastic exercise; so did the second on the fifth day; the third died of nervous exhaustion at the beginning of the seventh day while out riding. The origin of this story is unknown.

The pathological effects of prolonged complete insomnia are of great interest. Two cases were published by Agostini (1898): one a mechanic aged 45, who for six days and nights attended to the direction of his machine, owing to the absence of the companion who should have relieved him; the other, a young servant who attended to her sick mistress for many nights without taking any rest during the day. In both cases the symptoms were acute transitory amentia, with delirium, hallucinations, mental confusion, dulling of consciousness, and amnesia.

Weir Mitchell (1898) quoted 18 cases, the majority being students who sat up when preparing for examinations. They exhibited phenomena of grave insomnia with cerebral excitation, or of drowsiness prolonged for eight weeks, etc.

According to the researches of Dr. Marie de Manaceine (1894), Daddi (1898), and others, on dogs that died after enforced insomnia, marked disseminated alterations can be seen in the nerve-cells of the brain and spinal cord, and in the intervertebral ganglia.

The results of recent experiments by Legendre and Piéron (1911-12) are more accurate. In dogs kept awake till they showed an imperative need of sleep, there were alterations in the pyramidal nerve-cells in the motor region of the brain (chromatolysis, deformation of cell body, etc.). These lesions disappeared entirely if the animal was allowed to sleep. The urgent need of sleep after artificially prolonged wakefulness is—according to these authors—correlated with the development of a *hypnotoxic property* in the tissue-fluids, which when injected into the fourth ventricle of normal dogs produces the cellular lesions characteristic of insomnia as well as desire to sleep. This hypnotoxic action is more pronounced in the cerebro-spinal and cerebral fluids than in blood-serum. In all probability, therefore, it depends on the katabolites of cerebral activity.

These observations and experiments agree with the *chemical theory* of sleep, according to which fatigue, and the organic katabolism due to functional activity in the waking state, are the cause

or effective condition of sleep; and sleep is the phase of organic regeneration which determines awakening (Bichat, Joh. Müller).

The idea of "restorative" sleep is very ancient, and is even alluded to in Homer. It is a matter of common observation that fatigue induces the need of sleep; that sleep supervenes naturally after a certain time of waking or of work, and is usually the more irresistible and profound the longer the period of waking and the harder the work.

As the functional activity of waking accelerates katabolic processes and gives rise to a correlative amount of waste products, it is a natural corollary to assume that these waste products actually are the cause of sleep, inasmuch as they exert a hypnotic influence on the nerve-centres.

W. Preyer (1875-76) gave the name of *ponogenous substances* (fatigue products) to the katabolites that accumulate periodically in the blood during waking activity and produce the need of sleep. Whatever their origin and nature, these ponogenous substances are avid of oxygen, which they extract from the blood. Lack of oxygen in the blood produces that state of depression of the cerebral functions which is the essential phenomenon of sleep in the higher animals. According to Preyer, in fact, oxidation of the cerebral grey matter is indispensable to its activity in the waking state. Pflüger demonstrated this on the frog, and it has been confirmed by the latest studies on the metabolism of the nervous system by Verworn, Winterstein, and Baglioni (see Vol. III. p. 270).

The cause of the hypnosis produced by accumulation of the ponogenous substances has been interpreted in various ways by different authors. Rachel (1893) held that physiological sleep was due more to delayed elimination of these supposed poisons than to deficient oxidation of the nerve-centres. Errera (1891) assumed that the ponogenes are analogous to leucomaines, which were shown by Bouchard to have a narcotic action. Lahusen (1897) supposed that the activity of the nerve-centres produces narcotic autotoxin, which is destroyed during sleep. R. Dubois (1894-95) extended his conclusions on the hibernation of marmots to physiological sleep, and held that it consists in a carbonic auto-narcosis, *i.e.* on accumulated CO_2 in the blood. All these are variants of Preyer's hypothesis of *ponogenous substances*, which seems acceptable enough if we confine ourselves to their central nucleus, and leave aside the questions relating to their origin, nature, and mode of action, either upon the nervous system or upon other tissues.

But even when reduced to its simplest form, the theory of *ponogenous products* fails to explain a large number of facts connected with physiological sleep.

There is no parallel between the degree of exhaustion and the depth and duration of sleep; excessive fatigue frequently causes

insomnia. The new-born sleep more than adults, and old people more than young. It is difficult to co-ordinate these facts with the theory of a production of ponogenous substances during the activity of the waking state.

If we conclude that the decline in the depth of sleep is in ratio with the rate of elimination or destruction of the ponogenes, why does sleep not attain its maximum profundity when the accumulation of these substances is maximal, at the close of the long waking period? And why, after reaching its maximum after the first or second hour, does sleep decrease sharply and afterwards slowly to the moment of awakening, which is always preceded by a second slight rise in the curve?

How, on the chemical theory, are we to account for the hypnotising influence of darkness and silence, and, on the other hand, of monotonous sounds? How explain the fact that voluntary effort or preoccupation with some idea may delay sleep for several hours; while, on the other hand, indifference to the surroundings, passivity, or mere suggestion will suffice to induce sleep?

How does the chemical theory explain the phenomenon of prearranged waking? or that of partial sleep, during which the attention is on guard, focussed on a single object? How account for the obstinate insomnia of neurasthenics and maniacal dements, the profound sleep of some epileptics, the prolonged slumber of certain invalids, the very light sleep of some hysterical patients?

But granting that these objections prove the inadequacy of the chemical theory to account for all the phenomena of sleep, it is undeniable that even if the action on the brain of the ponogenous products developed during waking be not the determining and inevitable condition of sleep, it nevertheless constitutes its ordinary antecedent—*i.e.* the predisposing cause.

In order to complete the physiological account of sleep, it is necessary to take into account not only its *negative* aspect, represented by the depression of the external senses, atonia of the muscles, and suspension of the highest intellectual functions, but also its *positive* aspect, that is its restorative property. Just as the activity of waking predisposes to sleep, so the repose of sleep prepares for awakening.

It is important to note that the restorative efficacy of sleep is something more than and different from the mere functional rest of the organs of animal life, which may be obtained in the waking state. The interruption of the sensorial and psychical current by physiological sleep, if only for a few moments, will sometimes bring a renovation and flow of vitality into the nervous system which it is not possible to obtain while awake, even by lying down for hours in darkness and silence. Evidently in sleep the anabolic or assimilative processes prevail over the katabolic or dissimilative.

Physiological sleep is quite different from the *artificial narcosis*

produced by alcohol, ether, chloroform, or chloral hydrate. Verworn and his pupils showed that narcotics disturb oxidation in the nerve-cells, even when these cells are in extreme need of oxygen, as when fatigued, and they become unable to assimilate it. In sleep, on the contrary, the conditions are diametrically opposite to those of narcosis; it is by means of oxidative processes that the nerve-cells recover, and that the excitability of the system gradually rises to the level of the waking state.

Neither the fatigue of the ganglion cells in the waking state which predisposes to sleep, nor their recovery and recuperation during slumber, are, however, a sufficient basis for an adequate theory of the origin of sleep or awakening, although they express the nature of these in general and result physiologically from one or the other phase of daily life.

More prominence has, unfortunately, been given to the so-called *histological theory* of sleep, which is founded on the supposed amoeboidism or mobility of the neurodendrites. Among the supporters of this theory are Rabl-Ruckhard, Lépine, M. Duval, and Lugaro.

Lépine (1895) assumed that sleep was due to a retraction of the central terminations of the sensory neurones, and thus to their isolation from the neighbouring neurones; waking, on the contrary, being the result of re-established interneuronic contact. This, in his opinion, explains the instantaneous onset of and recovery from sensory or motor paralysis in certain hysterical subjects, and the fact that many normal persons can pass instantaneously from the waking to the sleeping state, and *vice versa*.

"In sleep," writes Duval, "the cerebral ramifications of the central sensory neurone are retracted, like the pseudopodia of an anaesthetised leucocyte, owing to absence of oxygen and excess of carbon dioxide. Feeble excitations of the sensory nerves provoke reflex reactions in the sleeper, but do not affect the cortical cells. Stronger stimuli provoke elongation of the cerebral ramifications of the central sensory neurones, and consequently the stimulus passes to the cortical cells, and the subject awakes."

This amoeboidism of the neurodendrites is not, however, founded on any positive observation, and was not accepted by Ramon y Cajal and Kölliker, the principal authorities on this subject, and the founders of the neurone theory. No amoeboid movement is visible, according to Kölliker, in the terminal appendages of the nerve-fibres, when these are observed in transparent parts of living animals. The axis-cylinder terminations of different nerve-organs present, according to Cajal, the same mode of connection by their respective dendrites in animals killed by chloroform or by bleeding or by poisoning, in such as were kept for a long time in rest or darkness, and in those fatigued before killing them.

Other authors (Rabl-Ruckhard, Demoor, Querton, and others) regarded the moniliform irregularities of the dendrites as a sign of shortening after fatigue, which interrupts the neuronic associations and produces sleep. But it was shown by Stefanowska that the moniliform appearance of the dendrites is a pathological symptom, and cannot be related to normal sleep.

Finally, according to Lugaro, in active states the only normal mobility of the neurones is a slight movement of the terminations; the varicosity of the dendrites is a pathological phenomenon due to fatigue or intoxication; the characteristic change in sleep is a general expansion of the tiny spines or gemmules of the dendrites; the retraction of these serves to isolate certain systems of neurones, to secure the momentary autonomy of the psychical associations, and thus to concentrate the attention upon certain groups of sensations or images. Nor does this exhaust the pack of hypotheses: according to Lugaro the expansion of the dendritic spines in sleep may be the effect either of the autotoxic action of the katabolites or of the inactivity of the nerve elements. Imagination is a precious gift in science when it serves to propound new problems and promote new researches; but its value is negligible when it is employed to build castles in the air from hypotheses which make a pretence of solving recondite physiological problems.

The same may be said of all the other partial theories of sleep, which are founded on a set of physiological or pathological facts, to which they give an arbitrary interpretation. Such, for instance, is the *secretory theory*, a reflex from the modern discoveries on the endocrinal glands, particularly the thyroid and hypophysis (Salmon, 1904-5); or the *osmotic theory* of Devaux (1906), according to which sleep is due to dehydration, owing to the increased viscosity of the blood!

None of the above theories, in attempting to explain the alternation of sleeping and waking, have taken into account the variations in its rhythm presented by different animals, which are largely due to the needs of defence, environmental conditions, the necessary hunt for food, etc. Why are some species and genera of animals (dogs, cats) able to sleep at any moment; why do others (rodents, herbivora) sleep very lightly; why have some (birds) the briefest possible sleep although their respiratory exchanges are extraordinarily active: why do some sleep by day and wake by night?

H. Foster (1900) and Brunelli (1903), from a high biological standpoint, insisted that in order to solve the problem of sleep it is necessary to study its genesis in the phylogenetic scale, and not rest content with analysing it in man "within the narrow limits of the cranium." According to Brunelli, sleep is a phenomenon of adaptation which is developed in the struggle for existence.

Following on these lines, Claparède (1905) attempted to formulate a *biological theory* of sleep, assigning to it the characters of an instinct. We should not sleep if sleep were not in some way beneficial to the organism. By means of daily sleep primitive man avoided the manifold sufferings to which he would be subject during the darkness of the night, and hereditary transmission rooted an imperative need of it in the race. Claparède holds sleep to be a *positive function*, and cites Cabanis, who wrote: "Sleep is not a purely passive state: it is a peculiar function of the brain which only occurs when a series of particular changes occur in it. Cessation of these brings about awakening, or the exterior causes of awaking produce it instantaneously." The same thesis was taken up and developed on different lines by Sergueyeff, Myers, Forel, and Vogt.

According to Claparède, sleep and waking are defensive functions, which come within the domain of biology, and are of great importance in the struggle for existence both in animals and man. "We sleep, not because we are poisoned or exhausted, but to avoid falling into these states." All tendency to sleep disappears in animals in the presence of danger, because a more general instinct of defence intervenes for the protection of the organism.

Waking too—according to Claparède—is controlled by the instinctive element of sleep. It is almost always provoked either by an external or internal feeling, or by a dream. But it may also be spontaneous when we no longer require sleep, "when slumber ceases to be the most important instinct of the moment." During sleep there is a not inconsiderable psychological activity, although it is difficult to analyse this because it is largely subconscious. In prearranged waking it is the voluntary resolution previous to sleep that works occultly during slumber, and causes the re-awaking. The cause of sleep is psychological; it consists in "the reaction of indifference to the present situation." The restorative effect of sleep is due to rest, to the elimination of toxic products before their accumulation becomes injurious, and to intensification of assimilative processes—"the relaxation of mental tension being probably compensated by an augmentation of the vegetative tension."

Claparède attempted to render a number of facts intelligible by this theory of the genesis and nature of waking and sleeping, but the transference of the problem from physiology to psychology by no means solves it. His ingenious endeavour nevertheless introduces us to the *psychological phenomenology* of sleep.[1]

VIII. From the psychological point of view sleep may

[1] The author is indebted to Professor G. Bilancioni for the exposition of the facts and theory of sleep in the above paragraph, as also for that which follows on *dreams*.

perhaps be regarded as a partial suspension of the highest psycho-physical processes, while the activity of the special centres, particularly the visual and auditory, and of internal common sensibility, is retained and even exaggerated.

Dreams are more or less plainly conscious manifestations of psychical activity during sleep. They result from a varied tissue of images, representations, and evanescent ideas loosely and irregularly woven together. The logical order is not infrequently reversed in dreams; associations which develop along collateral and unexpected paths build up ideas by contiguity and similarity. Even when the subject of the dream originates in an obscure sensation of the real world, it is often so remote from it as to make the psychical current absurd, incoherent, and chaotic. Nevertheless we distinguish in dreams, when they are sufficiently vivid, between the self and the not-self—that is between what can be referred to ourselves and what, really or by illusion, seems to relate to the external world. So, too, in dreams the distinction which is so clear in the waking state may persist between *presentations* and *representations*—that is, between the images that seem to be actual reality and the spurious or genuine memory images. We may therefore with P. Janet consider dreams to be a different orientation of the empirical personality—"an allotropic state of consciousness," or, in other words, a change of key in the mode of cerebral activity.

The methodical study of dreams presents many difficulties. The objective phenomena of a dream may be reduced to a minimum; to a mild imitation of the thing one is dreaming about, sometimes a word or sentence which gives a clue to the subject of the dream, accompanied or not by more or less elementary movements. In the rare cases in which dreams are associated with complex, co-ordinated movements, and these predominate over words, somnambulism results, which is, as it were, the staging and putting in action of the dream.

Dreams, accordingly, can only be studied by the subjective method—*i.e.* by *introspection*—with the inevitable twofold inconvenience that the observer is simultaneously subject and object, and that the matter for observation is not apprehended directly, but only as a record, which is always confused and distorted.

To lessen this inconvenience, Wundt advises that the dreamer should force himself, directly he awakes, to retrace and fix as firmly as possible the memory of the things dreamed about; should observe whether the momentary position of his body or other circumstances can account for the initial causes or favouring stimuli of the dream; should, in fact, compare the predominating images of the dream with the impressions and records of the day or of previous experience, whether recent or remote.

The experiment has also been tried of determining dreams

by impressing specific sensations of contact, temperature, light, tones or noises, etc., on the sleeper so as to furnish the materials for the construction of different dreams.

After many years of auto-observation, Hervey de Saint-Denys (1867) succeeded in acquiring a full memory of his own dreams, and collected a large number of facts. He held memory to be the prime element in dreams, and ascribed its importance to the sensorial and physical elements, which often act in the production of dreams independently of the will of the individual. It is certain that a great proportion of dreams are founded on the spontaneous recurrence of the records of the most important and recent, or even remote, events that have occurred in the waking state.

According to this author, dreams are characterised by the automatic development of a continuous chain of mnemonic images (*cliché souvenirs*) which are stored up as the mental heritage of the sleeper. Incidental extrinsic stimuli (sound, light) may introduce an extraneous idea into the oneiric current, which causes it to deviate. Attention and will may also intervene in dreaming; they are not necessarily suspended altogether during sleep. He claims to be able to alter and guide the oneiric current at will in given directions. By causing himself to be waked a number of times during sleep, he convinced himself that the vivacity and intensity of the images are always in ratio with the depth of sleep: the more profound the slumber, the more vivid and clear the oneiric images. This favours the theory that sleep is always accompanied by dreams, but auto-observations of Hervey de Saint-Denys on this point are completely opposed to other far more numerous records.

The method which might be termed *experimental dreaming* has been attempted with scanty result by many authors, both in healthy individuals and in pathological subjects—hysterical and epileptic.

Mourly Vold of Christiania (1896) covered one hand of a healthy subject with a glove, or bound up one leg, immediately before sleep. On waking, spontaneous or compulsory, he recorded the patient's dreams, and proved that they not infrequently originated in the state of the limbs. A student whose hand had been gloved during the night dreamt that he saw a hand issuing from an abdomen which had been opened, apparently for a surgical operation. Mourly insisted on the fact that the visual hallucinations, so common in dreams, may be incited by sensorial excitations of another modality. Cutaneo-muscular stimuli are of cardinal importance in promoting the visual hallucinations of dreams.

Stewart relates of a friend that having fallen asleep with a hot bottle at his feet, he dreamed of a journey to the crater of

Vesuvius and of his legs being scorched by the lava. In this case the unaccustomed sensation of warmth at his feet produced a complex oneiric current with a wealth of varied hallucinatory images.

Dreams are more often incited by *internal sensations of physiological needs* (hunger, thirst, desire to micturate, sexual impulse) than by external sensations.

Bierre de Boismont relates that in the thirst endured by the crucified in Jerusalem "they frequently dreamed" (oneiric imagination) "of the cool fountains of their native country." When Napoleon's army began to suffer from hunger in Russia, many soldiers were tormented by dreams of assuaging their appetite in their distant homes.

When the tension in the bladder produces the desire to micturate, nocturnal incontinence of urine occurs in children and also in certain adults, because they dream of voluntarily passing urine. Erotic dreams, which are so frequent in adolescence, are often caused by memories of the charmers of the previous day; but in celibates they are frequently due to the tension of the seminal vesicles, associated with hyperaemia of the genitalia, promoted by the warmth of the bed. When the erotic dream is accompanied by ejaculation the venereal paroxysm not infrequently produces awakening.

Dreams are to a large extent promoted by the hallucinatory images which, as we have seen, are not infrequently present in the drowsiness that precedes sound sleep (Maury's *hypnagogic hallucinations*) and in the waking-sleeping state that precedes awakening (Myers' *hypnopompic hallucinations*). Dreams dominated by visual hallucinations are the most frequent; those due to auditory hallucinations are less common; those started by tactile, gustatory, and olfactory sensations, still more rare. This difference in the frequency of hallucinations of the special senses is probably related to the ease with which the respective images are called up in memory.

From the psychological point of view more interest attaches to dreams produced by the functional state of the organs, both under normal and under pathological conditions.

Normally, the visceral functions do not give rise to any definite sensation in the waking state, although they participate in the formation of the common bodily sense or coenaesthesia. During sleep, on the contrary, the partial or total suspension of external sensations favours the development and increases the intensity of the internal sensations, and gives rise to a number of dreams. The dreams due to abnormal disorders of the viscera are particularly vivid, even before these are sufficiently pronounced to be noticed in the waking state. Aristotle, indeed, declared that incipient organic disorders might be manifested in dreams and be the precursors of disease.

Many authors, ancient and modern, have cited instances of such dreams. Galen speaks of a man with one leg paralysed, who had dreamt a few days previously that he had a leg of stone. Arnaldo di Villanova dreamed of a bite on one foot, and the following day an abscess developed there. Conrad Gessner, after dreaming that a serpent bit him in the side, was attacked by anthrax in that part. Pascal dreamt that he was being strangled with a noose, and two days later was seized with most violent angina. Alessandro Manzoni was half-awake, or perhaps experimented on himself, in one of these premonitory dreams, and took from it the idea of the uneasy dream of Don Rodrigo previous to the outbreak of bubonic plague, a dream that claims admiration for the profundity of artistic intuition and the delicate psychological analysis exhibited.

One of the most characteristic features in dreams is the rapidity with which events succeed each other, and give the dreamer the illusion of a time far exceeding the real period. Lorrain, Egger, and Clavière claim that the current of thought in dreams is far more rapid than waking thought. Piéron compares this rapidity of oneiric thought to the phenomena so often described of panoramic vision at the moment of death. The images called out by automatic cerebral activity and unbridled by attention pursue such a rapid course that sometimes if a sleeper is waked by two calls at a very short interval the effect of the voice invokes in his brain a dream which on waking seems to have occupied a very long period. Chamans, Comte de La Vallette, when in prison had a dream in the brief interval between the noise of opening the door of his dungeon and closing it again when the guard was changed, which in the dream appeared to him to have occupied a period of not less than five hours.

In a dream, owing to the absence of conflicting conditions, everything is amplified: the least sensation that invades the consciousness becomes the starting-point of a rapid series of images. "A flea bit me," writes Descartes, "and I dreamt of a sword-cut!" The very common illusion in a dream of falling to the bottom of an abyss may be due, according to Wundt, to the involuntary stretching of the sleeper's feet.

The commonly observed fact that a light sleep is often peopled with dreams of action suggested to Vaschide and Piéron that there is a certain relation between the depth of sleep and the tendency of the dream to go back into the past.

Undoubtedly some oneiric phenomena are not mere distorted memory images of the still vivid experiences of past life: memory is capable in sleep of calling up events that have been forgotten in the waking state. Brierre tells of a merchant who remembered in a dream the person to whom he had lent a sum of money six months before, whereas in the waking state he was quite unable

to recall it. It has often been noted that it is possible in sleep to recover minute details of distant events, as though impressions once received by the brain were never cancelled. Finally, in dreams we often picture places we have never seen, or events of which we are completely ignorant, or we develop ideas that never occur to us while awake. On the other hand, it is important to note that, according to a census taken by Stricker at the Hospital for the Blind in Vienna, those born blind never dream of seeing, but only of feeling and touching, and that for other blind people the visual images that appear in waking as well as in sleep are infrequent and blurred in proportion to the duration of the blindness.

It is a well-known fact that on waking we forget many of our dreams. The dreams we remember are generally those of the morning at the moment of waking, or when we are dozing off, previous to complete slumber. From this arises the belief that we do not dream for the whole time we are asleep. Goblot states that he is not acquainted with any history of a dream ending otherwise than in waking. A dream is "the commencement of awakening." He affirms that when near waking we are perfectly aware of it, and try to prolong a pleasant and to interrupt an unpleasant dream. In the first instance we try to avoid every possible cause of waking; in the second we wake purposely by making some movement or opening the eyelids.

The critical faculty is not altogether suspended in dreams: if the oneiric current assumes too absurd and unreasonable a form, if the hallucinatory images represent strange dangers, we are recalled to a sense of reality and set a limit to our dream; at other times, on the contrary, we imagine that we are awake while still sleeping. Sleeping and waking are sometimes confounded in consciousness, so that waking up appears to be a displacement of the field of attention.

It is interesting, again, to note that the oneiric current may sometimes present unconscious intervals, either in automatic dreams or in those suggested by peripheral or internal impressions. Interrupted dreams may be resumed many times and at long intervals. These afford valuable evidence as to the intermittency of consciousness in a long series of co-ordinated oneiric scenes.

Among the numerous attempts to formulate a theory of dreams, we need only refer to such as to some extent clear up the origin and psychical characters of the oneiric phenomenon.

Cullen first recognised the strong analogy between the dreams of sleepers and the hallucinations frequently observed in mental diseases and in certain infectious fevers. The different parts of the central nervous system, he says, slumber at different times in various degrees, thus causing a want of harmony in the psychical activity.

The analogy between the psychical structure of dreams and that of pathological mentation was next taken up by Cabanis, Lélut, and Moreau of Tours. The delirium of dements resembles a waking dream, just as the dream is the delirium of sleep. Hence we may reasonably consider dreams to be temporary madness. There is nothing in the phenomena of dreams that is not met with in the insane: predominance of visual and auditory hallucinations, exaggeration of memory, imaginary satisfaction of desires and aspirations, forced association of ideas, weak reasoning, loss of ideas of time and personality.

Alfred Maury, the eminent Hellenist, studied this subject at various times (1848–1878) and made a minute comparative analysis of dreams and the phenomena of insanity, in order to define their psychical affinity. Dreams, like the ideas of the insane, are, according to Maury, less incoherent than would appear at first sight: only the links between the ideas operate by irrational associations and by analogies that elude us on awaking. The extreme volubility of some insane persons betrays an acceleration of the psychical current which also characterises dreams. *Hypermnesia* and *paramnesia* are to be noted in madness and in the dreams of sleep. Finally, in dreams—according to Maury—we encounter all the symptoms of insanity.

In forming an adequate conception of the origin of dreams we must remember that our senses are not equally in abeyance in sleep, and that their normal functional equilibrium no longer exists; certain faculties disappear, others are exaggerated—and to this the dream is due. It arises from the hallucinations which Maury termed *hypnagogic*; its formative elements are usually memories, sensorial images, phrases, or impressions, acquired when we are awake, which present themselves in consciousness when the mind is no longer under rigid control and is unable to resist the incursion of fantastic sensations.

Another theory of dreams was put forward by Sigismund Freud of Vienna (1880). Starting from the *law of causality*, which governs the world of thought as it does the physical world, he applied it further to dream life. A dream, whatever it may be, is always the result of causes that pre-existed in the waking life; it is always a combination of elements that form part of our mental life, and finds its explanation in some previous psychical activity of the subject. The control which we exert over our acts and the course of our thoughts when awake is relaxed during sleep; the desires we seek to repress in the waking state have free play in dreaming. Oneiric representations often run counter not merely to the laws of logic, but also to the ethical principles of the individual.

When awake our thoughts follow in a sequence determined by certain connections of time or space, by suggestions or relations

due to some contrast or difference; in sleep these guiding threads to the course of our thoughts disappear, and similar or analogous images combine and reinforce each other. This results in fantastic groups of ideas, images, and emotions to which the bizarre and grotesque character of most of our dreams is due.

Some dreams—according to Freud—are founded on repressed aspirations and desires, and the hallucinatory images they present are only the symbolic clothing—often of a sexual character—of such desires. All dreams thus represent something significant in the life of the individual; we only dream what is worthy of being dreamt.

Without denying the partial truth of this conception of dreams, it does not seem to us acceptable as a general theory. Consciousness for the sleeper is an immense world, more vast perhaps than consciousness in the waking state. It is impossible to limit it by Freud's narrow formula. Not all dreams are important and significant; many, as we have seen, are produced by fortuitous external stimuli. Even in connection with representative dreams we cannot accept Freud's opinion unreservedly. To assume that dreams are the symbolical expression of some important motive in the life of the sleeper and are therefore physiological in character, conflicts with the fact that in sleep the power of perception and attention is very low, which again implies depression of will-power and of the faculty of perseverance to an end, and facilitates the invasion of the field of consciousness by a crowd of indifferent images.

Havelock Ellis (*World of Dreams*, 1911) proposed an ingenious psychological explanation of dreams, or rather of the great preponderance of visual images in dreams, which he refers to "sensory symbolism." By this he means the automatic transformation into visual imagery of sensory impressions of a different order (gustatory, olfactory, tactile, auditory, etc.). The visual impression becomes the symbol of another sensory impression; in other words, "a *symbol* means that two things of different orders have become so associated that one of them may be regarded as the sign and representative of the other." Coloured hearing, for instance, is a phenomenon of sensory symbolism. In dreaming, Havelock Ellis continues, "the usually coherent elements of our mental life are split up, and some of them are reconstituted into what seems to us an outside and objective world. An elementary source of this tendency to objectivation is to be found in the automatic impulse towards symbolism by means of which all sorts of feelings experienced by the dreamer become transformed into concrete visible images. . . . The conditions of dream life lend themselves with a peculiar facility to the formation of symbolism, that is to say of images which, while evoked by a definite stimulus, are themselves of a totally different order from that stimulus. The

very fact that we *sleep*, that is to say, that the avenues of sense which would normally supply the real image of corresponding order to the stimulus are more or less closed, renders symbolism inevitable. The direct channels being thus largely choked, other allied and parallel associations come into play, and since the control of attention and apperception is diminished, such play is often unimpeded. Symbolism is the natural and inevitable result of these conditions.

"It might still be asked why we do not in dreams more often recognise the actual source of the stimuli applied to us. . . . Here, however, we have to remember the tendency to magnification in dream imagery, a tendency which rests on the emotionality of dreams.[1] Emotion is naturally heightened in dreams. Every impression reaches sleeping consciousness through this emotional atmosphere, in an enlarged form, vaguer it may be, but more massive. The sleeping brain is thus not dealing with actual impressions, . . . even when actual impressions are being made upon it, but with transformed impressions. . . . Under these circumstances symbolism is quite inevitable. . . . The magnification of special isolated sensory impressions in dreaming consciousness is associated with a general bluntness, even an absolute quiescence, of the external sensory mechanism. One part of the organism, and it usually seems a visceral part, is thus apt to magnify its place in consciousness at the expense of the rest. As Vaschide and Piéron say, during sleep 'the internal sensations develop at the expense of the peripheral sensations.'" This, of course, gives rise to other forms of dream symbolism.

These and other partial explanations and interpretations of oneiric phenomena are very far from constituting a true scientific theory of dreams. But to a certain extent they clear up the confusion and mystery and bring out certain appreciable relations between the physiological activity of the different senses during sleep and the psychological activity connected with them.

IX. In speaking of dreams, we omitted to speak of another series of special phenomena occasionally manifested to us, which by their transcendental *ultra-* or *metaphysical* nature distinctly surpass the narrow limits of our scientific knowledge and appear to resist all rational interpretations. As such, they disturb the traditional orientation of the best scientific thought, but must not therefore be left out of account. Since the most severe criticism has failed, as we shall see, to demolish and invalidate them, every honest worker in science, every ardent and liberal inquirer into truth, must recognise the duty of taking cognisance of them, and of appreciating and insisting on their high philosophical value.

Myers propounded some original views of sleep and waking which form a suitable introduction to the consideration of tran-

[1] Vaschide also insists on the same point.

scendental oneiric phenomena. Sleep and waking, he says, are two alternating phases of personality, "differentiated alike from a primitive indifference, from a condition of lowly organisms, which merited the name neither of sleep nor of waking." He regards sleep as the primitive phase, as suggested by pre-natal and infantile life, the waking state being so far secondary and adventitious in that, even in adults, "it is maintained for short periods only, which we cannot artificially lengthen, being plainly unable to sustain itself without frequent recourse to that fuller influx of vitality which slumber brings."

"Out of slumber proceeds each fresh arousal and initiation of waking activities. To some extent at least the abeyance of the supraliminal life must be the liberation of the subliminal. To some extent the obscuration of the noon-day glare of man's waking consciousness must reveal the far-reaching faint corona of his unsuspected and impalpable powers."

This symbolic language in which Myers expresses deep philosophical ideas deserves a brief comment.

When the empirical or sensorial *ego* watches, dominates, and guides the current of thought, the intellectual mnemonic heritage of which the brain is the storehouse remains in great measure unutilised in the depths of the subconscious; when the light of consciousness is veiled, as in partial slumber, the capricious dominion of dreams prevails, and currents of sensations, memories, and thoughts mingle with the utmost rapidity and are more or less vivid or evanescent, according to the vagaries of the dream; when finally—as in deep sleep—consciousness is completely in abeyance, all the controls that dominate the energies of waking life are lost, while the subconscious operates more vigorously and freely to the advantage of the organism, though in occult ways.

This takes place normally in the common alternation of the two phases of our personality, represented by waking and sleep. But at times, in exceptional cases, in the semi-obscurity of dreams and the total obscurity of slumber, the mind displays supranormal faculties, and surpasses the most complex operations of which it is capable in the light of day—that is, when awake.

We have previously spoken of the visual hallucinations observed by some normal individuals (Cardano, Goethe, Johannes Müller) in the early phases of sleep, which A. Maury termed *hypnagogic* (illustrating them, as we have seen, by introspective observations), as well as of those that arise during the semi-waking state that precedes awakening, to which Myers gave the name of *hypnopompic*. These clear and vivid *subjective visions*, coloured like the figures seen on the screen of the photographic camera, are closely related to dreams. Maury's observations show, in fact, that hypnagogic hallucinations are sometimes represented in dreams—though they are less vivid and colourless; and hypno-

pompic hallucinations, according to Myers, are only the perfecting, at the moment when sleep is being dispersed, of the images seen in the dream. In both cases these hallucinations witness to an intensification of *internal vision* at the extreme phases of sleep, contiguous with waking, due to a state of hyperaesthesia of the cerebral vision, or better, to exaggerated activity of the cortical visual areas, aroused by internal stimuli of unknown character during incomplete sleep.

Visual hallucinations are common in the waking state among visionaries (such as, to take a classical example, the famous Scandinavian theosophist Swedenborg). They are most frequent in the insane, and form the basis of their delusions. Even under perfectly normal conditions, there is in the waking state a more or less obvious trace of the power of subjective vision. Every representation, or the evocation in memory of a visual image, suggests a rough draft, which is usually faint, evanescent, and obscure; sometimes, however, it is so vivid that painters can reproduce from memory the characteristic physiognomy of the people known to them. In "visuals," however, *i.e.* in certain predisposed individuals, these images in the initial and terminal phases of sleep assume the form of perfect hallucinations with all the characters of real visual images.

In "auditives," on the contrary, and primarily in musicians, it is the faculty of *internal hearing* that is specially prominent in sleep. Myers quotes certain cases of this; but the most classical example is the famous "Devil's Sonata" which the violinist Tartini heard in a dream while staying at the Franciscan Convent in Assisi, and partly transcribed, as best he could, on awaking. The French painter Marchal recorded this marvellous musical dream in a much-admired picture in the Gallery at Weimar.

These hallucinatory images—visual or auditory—probably, as Myers believed, constitute the highest point that the common sensorial faculties are capable of attaining, and it is remarkable that, normally, it is only reached in sleep.

The faculty of imagination, memory, and constructive ideal associations are also enhanced in sleep. Myers refers to the "admirable psychological insight" with which Robert Louis Stevenson described his own experiments in dreaming.[1] "By self-suggestion before sleep Stevenson could secure a visual and dramatic intensity of dream-representation, which furnished him with the motives for some of his most striking romances."

The well-known *inspiratory dreams* of Condillac, Cardano, Burdach, Lotze, Coleridge, Voltaire, and others arose in the same way. And not only imagination and memory, but also the power of ratiocination, calculation, and argument, may be intensified in dreaming. Cases are known in which problems have been solved

[1] *Across the Plains*, "A Chapter on Dreams." R. L. Stevenson.

in sleep, the solution of which was vainly sought in waking hours.

Further, in other, less frequent cases the exaltation of emotion and of all psychical activities during sleep may by a kind of involuntary auto-suggestion leave a permanent impress on the mind. These cases prove that dreams are sometimes capable of explaining an astonishing force begotten within the depths of our mental life which far exceeds anything the waking life can bring forth. Myers cites two main classes of this kind: "those, namely, where the dream has led to a 'conversion' or marked religious change; and those where it has been the starting-point of an 'insistent' idea, or of a fit of actual insanity." Instances of the first group are common in biographies of the saints (hagiographies), such as the conversion of St. Paul on the road to Damascus, which was due to a hypnagogic hallucination; those of the second are not rare in insanity. Taine relates a typical case where a gendarme was so impressed by an execution at which he assisted that he dreamed that he himself was to be guillotined, and was afterwards so obsessed by the dream that he attempted suicide.

However marvellous they may be, these phenomena are susceptible, given certain temperaments, certain precedents and physiological predispositions, certain histories of adolescence, of a naturalistic interpretation on the basis of common psychological criteria. Evidence of this is afforded by the subtle and remarkably clear psychological analysis in which A. Manzoni, without resorting to any mystical or miraculous intervention, provides a convincing explanation of the conversion of the "Innominato" in his immortal romance.

But when we pass on to consider *veridical hallucinations*, or *telepathic oneiric phenomena*, we really transcend the limit of our empirical consciousness, as acquired by way of the senses—a boundary that few scientific men have dared to pass, lest they should be reproached as credulous.

The first accurate investigations of the Society for Psychical Research (founded in London, 1882), and recorded in the famous *Phantasms of the Living* (1886) by Gurney, Myers, and Podmore, included about 150 telepathic phenomena in the form of dreams and another 100 in the form of well-attested hypnagogic hallucinations.[1] The great international inquiry undertaken by this Society between 1889 and 1894 ("Census of Hallucinations") led to surprising statistical results. The collection published by the astronomer Flammarion in his book *L'inconnu* yields another rich compendium of cases, though not always strictly controlled.

[1] Gurney and Myers first introduced the term "telepathy," which expresses their independent position, maintained on the one hand in relation to *spiritualists*, who lay more stress on their explanations than on the facts they profess to have proved; on the other, against *sceptics*, who claim to have destroyed the value of well-ascertained facts by the mere assertion that they were an impossibility.

Prof. Sante de Sanctis (1899) also contributed a valuable book *I sogni*, based on the clinical method of studying dreams. Lastly, in a remarkable number of periodicals devoted to the study of the so-called "spiritist phenomena," accounts are given of dreams and telepathic visions, which are very frequently collated with documents to prove their authenticity.

In the third International Congress of Psychology held at Munich (August 1896) a whole session was given up to a discussion on *telepathy*. The Congress considered the Report on the Census of Hallucinations undertaken in 1889 by a Committee of the Society for Psychical Research, the object of the inquiry being "to test whether the number of 'veridical hallucinations' (*i.e.* hallucinations representing some external fact) was or was not sufficiently numerous in proportion to the whole to preclude us from regarding as merely accidental the coincidence of fact and phantasm."

During the three years 1889-92, 17,000 persons were questioned, with due precautions against sources of error. The final conclusion was that there were about 30 death-coincidences out of 1300 cases, or a proportion of about 1 in 43.

In Myers' posthumous work, telepathic phenomena naturally constitute a corner-stone of the *new psychology*, which W. James termed romantic or Gothic in opposition to classical or academic psychology. Classical psychology may be compared to a coherent system of fine Greek architecture, but it contemplates only the superficial and fully conscious part of our mind, and completely ignores the deeper strata, the true underlying realities. The importance and originality of Myers' work in psychology is, according to James, that he brought forward the problem of the *subliminal*, which must be the chief preoccupation of the psychologists of the future.

After a scrupulous examination of certain concrete cases and special categories of veridical hallucinations (reciprocal, collective, etc.) Myers became convinced that they could not be explained on a physical hypothesis, or by any conceivable form of material or ethereal undulations or vibrations, such as might bring distant organisms into relation with one another. According to Myers, telepathy is a "psychical invasion," or direct intercommunication of minds, as already set forth by Christianity in the doctrine of the Communion of Saints. Telepathic phenomena prove that the mind of the agent, or rather certain parts of his subliminal personality, dissociated from the rest and detached from the body, may at times act from a distance upon the brain and thus upon the mind of the percipient. In less frequent cases the percipient again may influence all the persons within a certain range and thus produce the phenomenon of *collective hallucination*.

If we accept telepathy among the living as proven, then telepathy between the living and the dead becomes at least probable. According to Myers, observed facts justify this conclusion. Many cases of veridical hallucinations have been proved, either by their specific content, or by the moment of their production, to have emanated from people who were either at the point of death, or had already died some time before.

Myers held that the independence of mind and body is proved by cases of telepathy between the living, and the survival of the spirit after death by cases of telepathy between the living and the dead, and he attempted to develop this into a cosmic scheme in which science and philosophy and religion are combined. In this synthesis telepathy is extended into a universal law, a supreme cosmic truth, which unites all living beings, incarnate and discarnate, in this or other worlds, into one glorious universe of spiritual and moral life.

"Such a conception is strange indeed," exclaims Th. Flournoy, "when summarised thus in a few words and severed from its context, but it seems far less so, and becomes almost natural when described by the pen of Myers, and supported by certain facts—enveloped indeed by hypotheses, and yet so ingenious and sometimes so profound that it commands the admiration of the reader, and for a while compels his unquestioning assent."

Take, again, the verdict of a famous scientific man, who has scrupulously for twenty-five years applied to metaphysical problems the strict methods of research employed in solving the most arduous problems of physics. Speaking of telepathic phenomena, Sir Oliver Lodge affirms that "the evidence is so cumulative, and some of it is so well established, as to bear down the dead wall of scepticism in all those who have submitted to the drudgery of a study of the material. . . . I am prepared," he continues, "to confess that the weight of testimony is sufficient to satisfy my own mind that such things do undoubtedly occur. . . . We call the process telepathy—sympathy at a distance; we do not understand it. What is the medium of communication? Is it through the air, like the tuning-forks; or through the ether, like the magnets; or is it something non-physical, and exclusively psychical? No one as yet can tell you. We must know far more about it before we can answer that question—perhaps before we can be sure whether the question has a meaning or not. Undoubtedly the scientific attitude, after being forced to admit the fact, is to assume a physical medium, and to discover it and its processes if possible. When the attempt has failed, it will be time enough to enter upon fresh hypotheses.

"Meanwhile, plainly, telepathy strikes us as a spontaneous occurrence of that intercommunication between mind and mind (or brain and brain) which for want of a better term we at present

style thought-transference. . . . The opinion is justified by the fact that the spontaneously occurring impressions can be artificially and experimentally imitated by conscious attempts to produce them. . . . These experiments also want repeating. They require care, obviously; but they are very valuable pieces of evidence, and must contribute immensely to experimental psychology.

"What now is the meaning of this unexpected sympathetic resonance, this syntonic reverberation between minds? Is it conceivably the germ of a new sense, as it were—something which the human race is, in the progress of evolution, destined to receive in fuller measure? Or is it the relic of a faculty possessed by our animal ancestry before speech was? I have no wish to intrude speculations upon you, and I cannot answer these questions except in terms of speculation. I wish to assert nothing but what I believe to be solid and verifiable facts."

After an interesting discussion of experimental thought-transference, Lodge continues: "An attitude of keen and critical inquiry must continually be maintained, and in that sense any amount of scepticism is not only legitimate but necessary. The kind of scepticism I deprecate is not that which sternly questions and rigorously probes, it is rather that which confidently asserts and dogmatically denies; but this kind is not true scepticism, in the proper sense of the word, for it deters inquiry and forbids examination. It is too positive concerning the boundaries of knowledge and the line where superstition begins. . . .

"The whole of our knowledge and existence is shrouded in mystery: the commonplace is itself full of marvel, and the business of science is to overcome the forces of superstition by enlisting them in the service of genuine knowledge."[1]

Far too large a proportion of scientific men, however, scorn to occupy themselves with telepathic phenomena, because to them such problems only mean a retrogression, a recrudescence of mediaeval mysticism. They include under the heading mysticism those philosophical, spiritualist, or idealist tendencies which constitute the central, more or less conscious or subconscious, nucleus of human nature. For them Kant himself would be a mystic! The materialists of the nineteenth century went so far along this false track as to confound with mysticism—*i.e.* with the complex creeds and practices of superstition—the different forms of vitalism or physiological teleology professed implicitly or explicitly by the most illustrious biologists, past or present, in both the animal and the vegetable kingdoms.

When, after minute and patient experimental analysis of the physical, chemical, and morphological characters of the organism the physiologist—in order to embrace the whole phenomenology of Life—passes on to the study of the great biological laws,

[1] *The Survival of Man*, Sir Oliver Lodge, pp. 88 *et seq.*

and endeavours to give some explanation of the mysterious problems of heredity or the power of reproduction and evolution manifested by living substance, and of the different states of consciousness and subconsciousness, he readily admits that they are inexplicable by the laws of atomic and molecular mechanics, and feels the necessity of confronting materialism by vitalism.

Both *materialism*, or the atomistic hypothesis, and *vitalism*, the hypothesis of vital or psychical energy, must continue to function as indispensable vehicles, as the necessary poles of future physiological discovery.

"The evolutionary process of physiological science," as we said in the Introduction to Vol. I. of this work, "has always been in the past, and will always be in the future, a continuous and fruitful struggle between the two opposite tendencies of materialism and vitalism." Both are one-sided; each reflects only one aspect of the Real. The complete Theory of Life must be the result of their interpenetration and fusion.

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